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Benthic Organisms And Estuarine Communities Of The Southern California Bight

Bureau of Land Management
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INTRODUCTION TO POCS REFERENCE PAPER NO. III

The BLM-sponsored baseline studies have expanded the descriptive knowledge of the Southern California Bight, particularly, of the benthos, rocky and sandy intertidal areas to such an extent that the space allowed for the descriptive section of the OCS Sale No. 48 EIS was not adequate to even summarize this tremendous expansion of knowledge. In addition, over 250 benthic stations ranging over much of the Bight, including several areas being offered for lease in this sale, were examined for specimens but the results were not included in the report covering the study. Although the principal investigators of the study, Jones and Fauchald, examined these samples on their own initiative beyond the requirements of the contract, the data obtained could be important for BLM to evaluate potential impacts from the proposed sale. These stations, as well as those benthic stations reported are included in the reference paper on the benthos.

There were also some significant contributions in community classification in some of the most important estuaries of Southern California in the BLM study, so, because of this and their great importance, a reference paper was written on bays and estuaries.

Although marine macrophytes were included in both the kelp and intertidal sections, the brevity of the description sections negated a separate section on this important component of the Southern California marine ecology. For this reason, a brief overview was included on marine benthic algae.

POCS Reference Paper No. III was compiled and edited by Dr. Robert M. Gillard, Biological Oceanographer, Pacific Outer Continental Shelf Office, Los Angeles, California.

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A. Benthic Algae and Grasses

1. Introduction:

The following, with only minor changes, is taken from S. N. Murray (1974c).

The purpose of this chapter is to provide a summation and evaluation of published studies concerned with marine benthic algae and grasses of Southern California, i.e., the offshore waters including the eight Southern California Islands. Literature included in this report has been confined to that collected directly within the area, although attempts have been made to include additional relevant material where appropriate. Priority has been given to published studies deemed most important; therefore, an attempt has not been made to treat all published studies on the topic.

The great majority of the literature discussed has been concerned with macro-algae (Chlorophyta, Phaeophyta and Rhodophyta) and grasses (Spermatophyta) collectively referred to as macrophytes. Relatively little information exists on micro-algal components of the marine benthos, e.g., Cyanophyta (blue-green algae), benthic Bacillariophyta (diatoms) and benthic Chrysophyta (chrysophytes), for the Southern California region as well as worldwide. The contents of this report have been organized under the topics of taxonomy and ecology.

2. Taxonomy

a. General Floristics: The marine macrophytes from central California particularly near the Monterey Peninsula, are as well known as for any region of the Pacific Coast of North America (c.f., Smith, 1944; Hollenberg and Abbott, 1966). Knowledge of the marine macrophyte flora of Southern California, has recently been reported by Abbott and Hollenberg (1976).

Much of the knowledge of the algal flora of Southern California has been restricted to the mainland and gained from the works of W. A. Setchell (1912, 1914a, 1914b), N. L. Gardner (1913, 1917, 1926, 1927a, 1927b, 1927c, 1927d, 1927e, 1927f, 1940), Setchell and Gardner (1920, 1924, 1925, 1933), H. Kylin (1941), G. J. Hollenberg (1943, 1944, 1945, 1948, 1958, 1970, 1971), E. Y. Dawson (1941, 1946, 1949, 1950, 1952, 1954, 1957, 1958, 1960, 1961a, 1961b, 1962, 1963a, 1963b, 1966), and Dawson, Neushul and W. D. Wildman (1960). The Marine Algae of California (Abbott and Hollenberg, 1976), provides a much needed assimilation of taxonomic information of California algae including the algal flora of Southern California which is highly important in that it represents a common "baseline" for further taxonomic study.

Table 1 in Murray (1974c) provides a list of macrophyte species reported in Southern California including the eight Southern California Islands. This list has been prepared by the author with considerable assistance from Dr. Isabella Abbott (Hopkins Marine Station of Stanford University) and Dr. Thomas Widdowson (California State University, Long Beach).

b. Floristic Assemblages: Relatively little information exists with regard to floristic assemblages of Southern California. The most important works of this nature have been compiled for a few areas on the Southern California mainland (Dawson, 1945, 1959, 1965, 1966; Nicholson and Cimberg, 1971; Widdowson, 1971), certain of the Southern California islands (Dawson, 1949; Dawson and Neushul, 1966; Neushul, Clarke and Brown, 1967; Nicholson and Cimberg, 1971; Sims, 1974) and for kelp beds (Dawson, Neushul and Wildman, 1960; North, 1971). Table III.A-1 presents a compilation of the most common algal species of Southern California taken from Dawson (1959) and Table III.A-2 provides a list of seaweeds associated with Southern California kelp beds published by North (1971).

c. Southern California Islands: The eight Southern California Islands have been treated (Philbrick, 1967) as two groups, the Northern Channel Islands, consisting of San Miguel, Santa Rosa, Santa Cruz, and Anacapa; and the Southern Channel Islands including Santa Barbara, San Nicolas, Santa Catalina and San Clemente. These islands contain the only truly "pristine" marine communities that remain in the Southern California region. Additionally, the biota of the islands is extremely important to the understanding of the biogeography of the Pacific Coast of North America in that their location is along a major break in the marine environment at Point Conception. Presumably because of their relative inaccessibility, however, these islands have received very little scientific attention.

The benthic algae and marine grasses of the California Islands have not been adequately described. Dawson (1949) emphasized this point when he noted how extraordinary that a total of fewer than 20 species of algae had been reported from Southern California Islands prior to his work. Dawson indicated that 197 species of benthic algae had been identified; but reported on only the undescribed species and some of the more outstanding of his new records. Much of the floristic study has never appeared in the literature although some reports are included as range extensions in Dawson's works on (1952, 1954, 1960, 1961, 1962, 1963a, 1963b) the marine red algae of Pacific Mexico. Subsequently, additional information on the algal floras of these islands has been limited to collections of macrophytes from Anacapa Island (Dawson and Neushul, 1966; Clarke and Brown, 1967), San Clemente Island (Sims, 1974), and limited lists (Nicholson and Cimberg, 1971) of macrophytes from all but San Miguel Island. Several scattered reports (Silva, 1951, 1957; Chapman, 1961; Caplan and Boolootian, 1967; Foster, 1972) have provided little additional information on the macrophyte flora of the islands.

Table III.A-1

LIST OF THE 46 MOST COMMON MARINE PLANTS OF SOUTHERN CALIFORNIA IN ORDER OF RELATIVE FREQUENCY

Corallina vancouveriensis
Egregia laevigata
Gigartina canaliculata
Phyllospadix spp.
Gigartina leptrohynchos
Gastroclonium coulteri
Bossiella gardneri- dichotoma complex
Pterosiphonia dendroidea
Gelidium coulteri
Rhodoglossum affine
Gigartina spinosa
Chondria nidifica
Plocamium pacificum
Gelidium robustum
Smithora naiadum
Pelvetia fastigiata
Pterocladia capillacea
Ulva californica
Corallina officinalis v. *chilensis*
Chaetomorpha aerea
Centroceras clavulatum
Prionitis lanceoloata
Porphyra perforata
Lithothrix aspergillum
Melobesia mediocris
Enteromorpha compressa
Gracilariopsis sjoestedtii
Gelidium purpurascens
Laurencia pacifica
Pachydictyon coriaceum
Gymnogongrus leptophyllus
Ceramium eatonianum
Chondria decipiens
Gracilariopsis andersonii
Gigartina volans
Gelidium crinale v. *luxurians*
Nienburgia andersoniana
Gracilaria cunninghamii
Eisenia arborea
Cryptopleura violacea
Spermothamnion snyderae
Polysiphonia collinsii
Pterosiphonia baileyi
Hildenbrandia prototypus
Jania natalensis
Rhodymenia palmettiformis

Source: Dawson, 1959.

Table III.A-2

MACROPHYTE SPECIES OF SOUTHERN CALIFORNIA AND NORTHERN BAJA CALIFORNIA KELP BEDS

SPERMATOPHYTA

*Phyllospadix torreyi

CHLOROPHYTA

Chaetomorpha spiralis
Cladophora graminea
Codium cuneatum
Codium hubbsii
Codium setchellii
"Halicystis ovalis"

PHAEOPHYTA

Agarum fimbriatum
Coilodesme californica
Coilodesme rigida
Colpomenia sinuosa
*Cystoseira osmundacea
Cystoseira setchellii
Desmarestia ligulata var. ligulata
Desmarestia tabacoides
Dictyota binghamiae
*Dictyota flabellata
Dictyopteris undulata
*Egregia menziesii
*Eisenia arborea
Giffordia granulosa
Halidrys dioica
*Laminaria farlowii
Laminaria setchellii
Macrocystis pyrifera
Nereocystis leutkeana
Pachydictyon coriaceum
Padina durvillaei
*Pelagophycus porra
*Pterygophora californica
Sargassum agardhianum
Taonia lennebackerae
*Zonaria farlowii

RHODOPHYTA

*Acrosorium uncinatum
Amphiroa zonata

Table III.A-2 (Cont.)

Amplisiphonia pacifica
Anisocladella pacifica
Antithamnionella glandulifera
Binghamia forkii
*Bossiella orbigniana ssp. dichotoma
*Bossiella orbigniana ssp. orbigniana
Botryocladia neushulii
Botryocladia pseudodichotoma
Botryoglossum farlowianum
Branchioglossum undulatum
*Calliarthron cheilosporioides
*Calliarthron tuberculosum
Callithamnion sp.
Callophyllis firma
Callophyllis flabellulata
Callophyllis violacea
Carpopeltis bushiae
Ceramium pacificum
Chondria californica
Chondria nidifica
*Corallina officinalis var. chilensis
*Coralline vancouveriensis
Cryptonemia angustata
Cryptonemia obovata
Cryptopleura crispa
Cryptopleura violacea
Fauchea lacinata
Fryeela gardneri
Gastroclonium coulteri
Gelidium nudifrons
Gelidium robustum
Gelidium purpurascens
Gigartina canaliculata
Gigartina corymbifera
Gigartina serrata
Gigartina spinosa
Gigartina volans
Gracilaria sjoestedtii
Gracilaria textorii var. cunninghamii
Gracilariophila oryzoides
Grateloupia howeii
Grateloupia schizophylla
Griffithsia pacifica
Gymnogongrus leptophyllus
Haliptylon gracilis
Laurencia spectabilis var. diegoensis
Laurencia splendens
Laurencia subopposita
Leptocladia binghamiae
Lithophyllum imitans
Lithothamnium giganteum

Table III.A-2 (Cont.)

Lithothrix aspergillum
Maripelta rotata
Melobesia mediocris
Mesophyllum lamellatum
Microcladia coulteri
Myriogramme caespitosa
Neoagardhiella baileyi
*Peyssonelia rubra
Phyllophora californica
Phyllophora clevelandii
*Plocamium cartilagineum
Pogonophorella californica
Polyneura latissima
Polysiphonia johnstonii
Polysiphonia mollis
Prionitis andersoniana
Prionitis cornea
Prionitis lanceolata
Prionitis linearis
Pseudogloiophloea confusa
Pterochondria woodii var. pygmaea
Pterochondria woodii var. woodii
Pterocladia capillacea
Pterosiphonia baileyi
Pterosiphonia dendroidea
Rhodymenia arborescens
Rhodymenia californica var. attenuata
Rhodymenia californica var. californica
*Rhodymenia pacifica
Schizymenia pacifica
Sciadophycus stellatus
Scinaea johnstoniae
Smithora naiadum
Stenogramme interrupta
Tenarea dispar
Tiffaniella snyderae

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*Species marked with an asterisk are considered to be common in kelp beds.

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3. Ecology

a. General Information: Studies of the ecology of communities of benthic macrophytes performed in the Southern California region are few in number. Few studies have been performed on intertidal macrophytes; however, the algal communities of the nearshore benthos, particularly those associated with the giant kelp beds, have received considerable attention.

b. Intertidal Ecology

i. Southern California Mainland: Sandy beaches have their complement of vegetation in the form of kelp and other algae and plankton washed ashore in addition to bottom microscopic plants (mostly diatoms) living within the spaces between sand grains. Although the majority of the mainland shores consist of sandy beaches, these floral assemblages are more transient, and far less studied than the rocky shore flora.

Ecological studies of intertidal communities of Southern California are quite few in number. Of the limited information available, the most useful appears to be that concerned with communities of macrophytes (Dawson, 1959, 1960; Widdowson, 1971; Nicholson and Cimberg, 1971). Dawson (1959, 1965) surveyed a number of rocky intertidal stations in Southern California from 1956-1959 in an attempt to construct records of the distribution and abundance of the more conspicuous macroscopic algae. His efforts were part of a California State Water Pollution Control Board project, initiated in 1954, concerned with methods and effects of the disposal of sewage into the sea.

Prior to Dawson's studies, the only usable information for comparisons was contained in the collections of intertidal algae gathered between 1895 and 1912 by W. A. Setchell and N. L. Gardner from three rocky areas (Whites Point, Sunset Blvd. Beach, and Point Fermin) in Los Angeles County. After examining these collections, Dawson (1959) concluded that approximately a 50 to 70 percent reduction in the number of species comprising the algal floras at the Whites Point and Sunset Blvd. sites had occurred, whereas little change was evident at Point Fermin. In that the Whites Point and Sunset Blvd. stations were subject to a high degree of sewage pollution, Dawson attributed the observed declines to sewage effects. Further, Dawson (1959) reported that several species of articulated coralline algae were capable of development within close proximity to marine sewage outfalls.

To expand on Murray's summary of Dawson's study, the Allan Hancock Foundation (1965) summarized some seasonal and vertical observations of the intertidal flora. It was apparent that there were marked seasonal changes in the composition of the flora, more so in some areas than in

others. The maturity of certain dominant species may, at some seasons, completely change the appearance of the flora. In other instances, seasonal changes in the sand deposits of an area may markedly affect the flora by altering the substrate, sometimes by the complete burial of the algal inhabitants of the rock outcrops for several months. The annual cycles, however, are subject to great variation from year to year, and in a given area the local ecological variables may partly or largely overrule the general annual cycle. Accordingly, in making seasonal observations over a period of a few years at a large number of localities, one is impressed almost as much by the annual variations as the seasonal ones.

Nevertheless, comparisons of the seasonal observations at 39 stations visited twice or more permits the following generalities to be made: 1) In gross aspect the Southern California benthic algae does not show conspicuous seasonal differences in quantity or quality. Most of the larger dominant species are present throughout the year, although the luxuriance, age, and condition of the plants may show considerable seasonal variation. 2) It is in the upper levels of the intertidal region, partly subject to shifting sand, that marked seasonal growth and decline of colonies of annual plants, such as *Entermorpha, Ulva, Porphyra, Chaetomorpha*, etc., are commonly noted. 3) In the lower intertidal and infratidal areas, seasonal variation in composition of the flora is confined largely to species which are not large members of the flora. Thus, a number of annual species may appear during the spring and summer, augmenting the principal vegetation which remains throughout the year. 4) At most stations, the flora as a whole shows a decline in growth and luxuriance during the summer and fall. Most annual species reach their peaks in summer or early fall, and a few annuals mature in winter or spring.

At the lower levels of the intertidal zone which are uncovered only occasionally or not at all, attached algae tends to become more profuse and according to Ricketts, et al., (1968), working in Central California, the large kelp *Laminaria* and the seed plant *Phyllospadix* (eel grass) become the most dominant forms. In an attempt to describe changes in the algal composition of the Southern California intertidal, Widdowson (1971) surveyed several of Dawson's original stations. Widdowson's study revealed a general and widespread decline in the marine intertidal flora near Los Angeles since 1956-1959. Sewage pollution was also implicated although the degree to which a station was exposed to human traffic was reported to be more highly correlated with floral decline.

Subsequent to the 1969 Santa Barbara oil spills, several studies (e.g., Straughn, 1971; Foster, Zingmark and Neushul, 1970) were initiated to determine the effects of oil on marine populations. Nicholson and Cimberg (1971) surveyed 10 Southern California stations (8 corresponded to those of Dawson) in an attempt to evaluate the effects of oil on

rocky intertidal populations. The results of their studies supported the conclusions of Widdowson (1971) in that a reduction in the variety of species in the Southern California intertidal algal flora had occurred. Comparisons between patterns of species distribution also revealed (Nicholson and Cimberg, 1971) that certain green algae, characteristic of environments rich in organic chemicals were more abundant in 1969-70 than in 1956-59. The presence of systems for the uptake of amino acids in *Ulva, Corallina* and *Gelidium*, all of which have been reported (Nicholson and Cimber, 1971; Widdowson, 1971) to be abundant in Southern California, have been demonstrated and implicated (Stephens and North, 1972) in the success of these algae in sewage-polluted environments.

ii. Southern California Islands: Ecological work on intertidal communities of the Southern California Islands has been limited to studies of San Nicolas (Caplan and Boolootian, 1967), Santa Cruz (Hewatt, 1946) and San Clemente (Murray and Littler, 1974a). The biota of each of these islands is somewhat different (Neushul, Clarke and Brown, 1967) with San Nicolas being strongly influenced by the cold California Current whereas Santa Cruz receives both cold water from the California Current and warmer water from the south; San Clemente Island is bathed primarily by warmer southern waters.

Caplan and Boolootian performed a study of the littoral ecology of two rocky areas on San Nicolas Island in June of 1964. Their report included contributions of only 19 macrophyte species and omitted a goodly portion of the intertidal region (+2.0 ft.). Conclusions of this study revealed that the flora and fauna of the intertidal region were representative of both northern and Southern California associations and that the dominant species in each intertidal zone were also similar to mainland species.

In the summer of 1939, W. G. Hewatt stayed on Santa Cruz Island, and established species lists for Scorpion Harbor, Smuggler's Cove, Pelican Bay, Prisoner's Harbor, Christy Harbor, and Wellis Harbor. These collections, however, included only faunistic components and, other than for a few passing remarks, species of macrophytes were omitted.

Studies by Murray and Littler (1974a) have been carried out since June, 1971 on marine intertidal communities of Wilson Cove, San Clemente Island. These studies have involved general floristics, analyses of standing stock and primary productivity of communities under the influence of sewage stress from the local U.S. Navy base and of nearby control regions.

The low volume sewage discharge (20-25,000 gal/day) altered (Murray and Littler, 1974b) species composition and reduced spatial heterogeneity and species diversity of macrophyte-dominated intertidal communities on leeward San Clemente Island, California. A total of 13 species, which

provided 91.7 percent cover, were recorded for the sewage-affected area while 30 species and 100-percent cover occurred in neighboring control areas. The brown algae, *Egregia laevigata, Halidrys dioica* and *Sargassum agardhianum*, the angiosperm *Phyllospadix torreyi* and the crustose coralline *Lithophyllum decipiens* were conspicuously absent from the outfall region; these species contributed approximately 35 percent of the cover of control area intertidal communities. Cover of blue-green algae, *Ulva californica, Gelidium pusillum* and *Pterocladia capillacea* was significantly enhanced in the outfall area while that of *Gigartina canaliculata* decreased. A great reduction in stratification and, hence, spatial heterogeneity, primarily due to the absence of large brown algae and *P. torreyi*, occurred in the sewage-affected area, where a low turf consisting of blue-green algae, *U. californica, G. pusillum* and small plants of *P. capillacea* was found in similar tidal intervals. Simple species counts and four different quantitative indices revealed that the diversity of control area communities was considerably greater than that of the outfall region.

The total primary productivity of the intertidal macrophyte community under sewage stress (127.1 mg C/m^2 per hr) was not (Littler and Murray, 1974) significantly different from that of nearby control (non-polluted) communities (125.4 mg C/m^2 per hr) even though there was 8 percent less cover and about half as many species near the outfall plume. The intertidal macrophytes on leeward San Clemente Island, California, produce approximately 485 net g C/m^2 per year, a rate comparable to that reported for most marine communities. No apparent relationship was revealed between the productivity of an alga and the division to which it belongs; however, productivity was associated with growth form. Encrusting prostrate forms were the lowest producers in terms of g C/m^2 per hr and g C/g dry wt per hr; sheet-like and finely-branched forms showed a greater productivity than coarsely-branched forms. *Gelidium pusillum* and *Ulva californica*, associated with the disturbed outfall area, show considerably greater productivity per unit of thallus area than any of the other algae measured.

Obviously there is risk in extrapolating short term productivity rates to daily or yearly rates.

c. Subtidal Ecology

i. Southern California Mainland: The majority of literature on the ecology of subtidal macrophyte communities has been gathered on kelp bed communities. The dominant plant comprising Southern California kelp beds is *Macrocystis pyrifera*. Along the inward border of a typical Southern California kelp bed, *Egregia* becomes dominant whereas at the outer edge, *Pelagophycus* becomes the most conspicuous plant. Surf grass (*Phyllospadix*) and several medium

sized brown algae (*Eisenia, Pterygophora, Laminaria*, and *Desmarestia*) occur from the intertidal to almost the outer fringes of the large floating kelps, especially in areas of clear water.

Beneath these forms, a number of smaller green, brown, and red algae become common. The marine flora associated with kelp beds is fairly well known. North (1971) has compiled a list of the plants associated with Southern California and northern Baja California kelps (Table III.A-2) This table was compiled from personal observations by North and works by Smith (1944); Limbaugh (1955), Turner, et al., (1964a, b, 1965); McClean (1962) and Dawson, Neushul and Wildman (1960).

Macrocystis is distributed (North, 1972) in boreal and temperate waters near every major land mass in the southern hemisphere and along the Pacific coast of North America from Alaska to Punta San Hipolito in central Baja California. North (1971) has hypothesized that the world-wide distribution of the genus is limited by temperature since *Macrocystis* is absent from the tropics. Three species of *Macrocystis* have been listed from California waters, *M. integrifolia* Bory, *M. pyrifera* (Linnaeus) Agardh and *M. angustifolia* Bory (Womersley) (North, 1971). The morphology and physiology of plants is highly variable; *Macrocystis pyrifera* from Southern California, for example, does poorly at temperatures exceeding 20°C whereas 600 km south, populations of *M. pyrifera* flourish in water that reaches 26°C in later summer (North, 1957). Capabilities of the two *Macrocystis* populations also differ (Clendenning, 1958). Clendenning (1971) has reported an annual organic production for a "good" kelp bed of 6.50 to 6.65 tons per acre-year. Visual No. 2 shows the kelp beds of Southern California.

ii. Southern California Islands: The subtidal ecology of the California Islands has been poorly studied. Studies of subtidal plant and animal communities of Anacapa Island (Neushul, Clarke, and Brown, 1967) have helped portray the distribution of dominant plant and animal species in nearshore kelp beds and provided information on the biogeographical status of plant and animal species. The stress of currents applied to large plants was discussed; later work on *Eisenia* (Charters, et al., 1972) being a follow-up to these observations. Algal turf constituents of the nests of *Hypsypops rubicunda*, the ocean goldfish have been described for populations at Coches Prietos, Santa Cruz Island.

The University of Southern California Allan Hancock Foundation has conducted a systematic survey of the marine biota of Santa Catalina Island in conjunction with the marine laboratory there. These surveys are in progress and should provide additional information on nearshore ecology.

iii. Kelp-bed Research Programs: Since the early 1950's, the kelp beds of Southern California have received a great deal of scientific attention. North (1968) has described the historical development of much of these efforts prior to 1968. These can be summarized (largely after North, 1968) as follows:

During the early part of the 1950's the dwindling kelp beds of the Southern California region attracted much general concern. Causes for the general, well-documented reduction of beds could only be speculated; however, detrimental effects of harvesting activities and pollution were most frequently discussed. These matters came to the attention of the California State Legislature and the State Department of Fish and Game. A State Kelp Study Committee was subsequently formed to advise the California Fish and Game Commission. The committee concluded that much basic biological knowledge was necessary before any proper decisions could be made and recommended a large scale research program on kelp to be undertaken.

The Kelp Investigations Program was established as an outgrowth of this recommendation and received funds from the Department of Fish and Game, the State Water Quality Control Board, and the National Science Foundation for pursuing kelp studies.

These research efforts became known as the IMR Kelp Program and lasted from 1956 to 1963 during which a number of progress reports and three large publications, An Investigation of the Effects of Discharged Wastes on Kelp (State Water Quality Control Board, 1964); Utilization of Kelp-Bed Resources in Southern California (North and Hubbs, 1968) and The Biology of Giant Kelp Beds (*Macrocystis*) in California (North, 1971) resulted.

One of the principal findings of the IMR program was that excessive grazing by large populations of sea urchins were destroying the remains of several important Southern California Kelp Beds. A second project, The "Kelp Habitat Improvement Project" was first funded in 1962 to determine if these urchin populations could be controlled. This project is yet active and has expanded geographically from San Diego to Orange and Los Angeles Counties. It has been supported since its inception by grants from the Kelco Company of San Diego (a Kelp Harvesting concern). Additional monies have been received from the Fish and Game Commissions of San Diego, Orange, and Los Angeles Counties (since 1965 and 1966), Ocean Labs, Inc., of Irvine, Ca. (since 1969), Office of Sea Grants, U.S. Department of Commerce (1968, 1970, 1972), Los Angeles Rod and Reel Club Foundation (1970) and the Balboa Angling Club (1972). The Kelp Habitat Improvement project began at the Institute of Marine Resources and has continued at the California Institute of Technology

since 1964. Dr. Wheeler J. North has been the principal investigator since the project's inception and much of its success can certainly be attributable to his energies and excellent direction.

The following summaries of the Kelp Habitat Improvement Project have been given in a recent annual report (1971-72).

San Diego County. The project began operations in San Diego County in September of 1962 with initial work being directed towards the control of urchin populations with quicklime off Point Loma. Lesser efforts were made to restore kelp beds at La Jolla and barren Imperial Beach. The principal factor found to hinder *Macrocystis* expansion at Point Loma was grazing by sea urchins. Through programs directed at urchin control the Point Loma beds were restored to 50 percent of their maximum area by 1967.

The La Jolla kelp beds received increased attention after 1967. Grazing pressure from urchins and the occupancy of bottom territory by other smaller kelps were viewed as the factors preventing the establishment of *Macrocystis*. Programs of urchin monitoring and control and the dispersal of cultures of embryonic *Macrocystis* succeeded in restoring approximately 10 percent of the former maximum kelp coverage. In 1963, 1965-67, small colonies of *Macrocystis* were established from transplants in the Imperial Beach region. These, however, were overrun by urchins. In 1970, the Imperial Beach Kelp restoration activities were accorded top priority. Urchin monitoring and clearing activities and the dispersal of embryonic and juvenile sporophyte plants of *Macrocystis* have been carried out. Through these efforts, 200 attached and transplanted plants, some 10-20 feet high, composed the Imperial Beach kelp stand by the end of June, 1972.

Orange County. The program in Orange County has consisted of transplantation of adult *Macrocystis*, dispersal of cultures of embryonic sporophytes and the control of populations of sea urchins. Initial operations, begun in 1967, were to restore kelp within 5 miles of coast between Laguna Beach and Corona del Mar. These efforts have been highly successful as indicated by the fact that the Laguna-Corona del Mar kelp beds represent the only beds within the County that have shown a trend other than general deterioration during the past 14 years. *Macrocystis* stands now occur almost continuously in the area although many of the plants are young and have yet to produce a surface canopy. The large kelp beds that occurred from Dana Point south to San Mateo Point were once the largest in the County. These have been reduced drastically and now consist of only small well-spread patches. Kelp restoration activities were initiated off Dana Point in 1972.

Los Angeles County. The fifth year of kelp bed restoration activities in Los Angeles County was completed in 1971-72; these operations have been directed towards the Palos Verdes coastline where 30 years previously,

extensive beds ringed the entire peninsula. Activities have included the transplantation of kelps from Southern California beds to Abalone Point and Whites Point on the Palos Verdes peninsula, introduction of cultured juvenile sporophytes, dispersals of cultured embryos, urchin monitoring and control, and control programs for grazing fishes. As of 1972, a relatively small crop of plants (50 adult transplants and 50 juveniles plus several dozen younger plants) has been protected at Abalone Cove, the site of most efforts.

In 1970, members of the Ocean Fish Protective Association conceived a plan for enhancing the Palos Verdes nearshore in addition to work being performed as part of the Kelp Habitat Improvement Project. This work involved efforts at controlling the dense populations of urchins occurring along the Palos Verdes peninsula. The aid of amateur divers of Los Angeles was solicited in this regard. In August of 1971, 700 amateur divers using hammers, etc., spent the day reducing the urchin populations at Whites Point in water 6 to 9 m (20 to 30 feet) deep. In the ensuing months, growth of algae appeared in areas where urchin populations had been decimated; subsequent operations have attempted to further the aim of reducing urchin populations and thereby created areas for seaweed development.

It is quite clear that the "kelp projects" have received a high degree of priority from Federal, State and local agencies. Much work and the expenditure of large sums of money has occurred in attempts to understand and prevent kelp bed deterioration. These programs have been surprisingly successful and have gathered some of the best information available worldwide on the *in-situ* ecology of the large kelps.

B. Benthos

The invertebrate benthos, largely based on a paper by Bright (1974), is covered in greater detail in the BLM (1975) Sale No. 35 EIS. The recent studies by Jones and Fauchald (1977) on subtidal benthos, Straughan (1977) on the sandy beach intertidal, and Littler (1977) on the rocky shore intertidal have added significantly to the knowledge of invertebrate benthic organisms and communities in the Southern California Bight.

Emery (1960) divided the Southern California offshore area into the mainland shelf (from the mainland coast to the 100 m (300 feet) contour line) and the continental borderland (from 100 m (300 feet) contour line to the Patton Escarpment 80 km to 241 km (50 to 150 miles) offshore). These terms will be used throughout this narrative.

The benthos of the California Bight is extremely complex, consisting of many species and assemblages, and is difficult to summarize. Some of the reasons for this complexity are: 1) the numerous available habitats allowed by the topography of the continental borderland consisting of islands, deep basins, submarine canyons, and the resulting sediment complexity; 2) The relatively stable temperature and salinity conditions favor a biologically accommodated system consisting of many species (Sanders, 1968); 3) The Bight area is a biogeographic transition zone between the Californian and Oregonian Provinces with the division line at Point Conception (Valentine, 1966). Because the water temperatures and other factors are often typical of both provinces, the Bight has species of the Oregonian Province to the north, and the Californian Province, as well as species which are only found in the Southern California Bight. Valentine (1966), for example, reported 180 species of Bivalvia and Gastropoda, alone, had a north-south geographic range of only 96 km (60 miles) within the Bight area.

Simply, one may apply the concept of Peterson and Thornson that a benthic assemblage can be characterized by one to several dominant species (Thorson, 1957). The dominant macrobenthic species of these communities woud be distributed within a given geographic area by depth and sediment type and the predominating animals will belong to the same genera in different geographic areas under similar environmental conditions. This concept has been questioned lately. Actually, there is no consideration of the smaller, more numerous benthic community members.

Recent thinking largely conceives the benthos as a loosely bound association rather than a discrete assemblage with animals either bound together by biological interactions or determined by precise limits of the environment. Rather, the associations consist of organisms which

have similar reactions to their environment, physical and biological, and, as a result, are found within the same geographic area in roughly the same habitat. The assemblage, in either case, will consist, not of one or several dominants, but of many species.

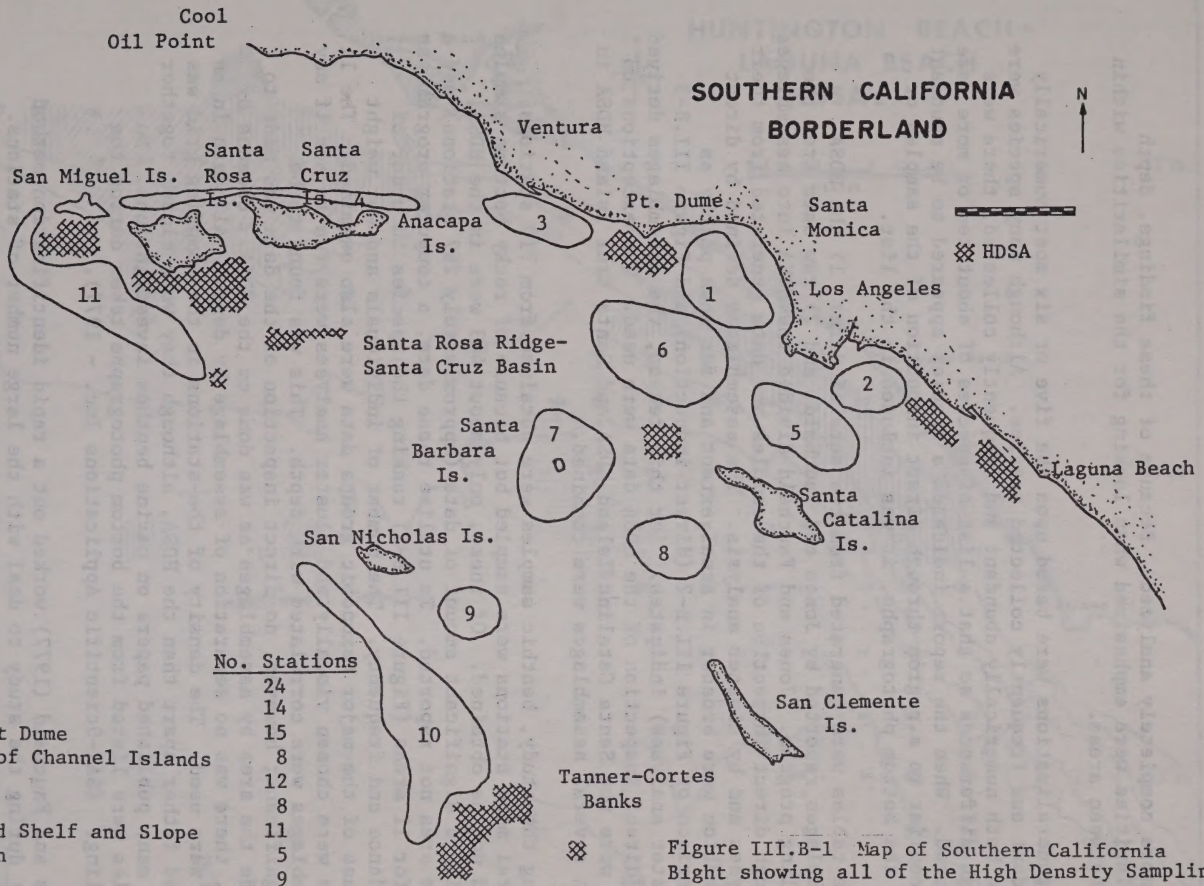
The designation of an area according to dominant species is convenient and may, particularly if the association members are identified and known, signify a high degree of understanding of the area in certain cases.

Most of the major benthic habitats within the Bight have been sampled. The principal studies have been Hartman and Barnard (1960) of the basins, Hartman (1963) of the canyons, Allan Hancock Foundation (1965) and Jones (1969), of the mainland shelves. The island shelves, until recently were apparently only reported from ten samples taken near Santa Catalina Island (Mattox, 1955). Rocky bottoms have been studied at one location off Corona del Mar (Pequengant 1963, 1964 and 1968) and at Tanner-Cortes Banks by BLM personnel.

During 1975, BLM sponsored a subtidal soft bottom benthic survey which recorded the associations of seven intensively sampled areas; including the mainland shelf, island shelves, a basin, and their respective slopes (Visual No. 7). A more extensive sampling grid was utilized (Figure III.B-1), but the associations were not reported Jones and Fauchald, 1977). The study involved the most extensive investigations ever made of the biota of each major type of habitat in the Bight and is rivaled in scope only by the State Project (Allan Hancock, 1965).

In spite of these intensive efforts, Visual No. 7 indicates the amount of area defined in relation to the total Bight is relatively small. The data from all the above soft bottom studies were primarily obtained with a "grab" of core which blindly brings up a small amount of bottom. This is roughly equivalent to dropping a steam shovel on earth from above a heavy cloud cover; a relatively small portion of the bottom is examined and there is a chance of missing significant structures and organisms. A picture taken concurrently with every core helped define the sediment surface associates, but was still extremely limited in areal coverage.

The data from the BLM study are reported in simplified form in Tables III.B-1 through III.B-9, III.B-11 through III.B-19, and III.B-24 through III.B-34. An attempt was made to generalize the data and to portray broad similarities between the areas. Jones and Fauchald (1977) indicated the single most important environmental variable governing the distribution of species within nearly every high density sampling area (HDSA) was depth. It appeared to be significantly more important than sediment and areal location, at least on the shelves and slopes. Although these other variables exerted significant influence at some locations, they may be found to be more important when the data



	No. Stations
Santa Monica Bay	24
San Pedro Shelf	14
Shelf north of Point Dume	15
Island Shelf North of Channel Islands	8
San Pedro Basin	12
Santa Monica Basin	8
Santa Barbara Island Shelf and Slope	11
Santa Catalina Basin	5
San Nicolas Basin	9
Southern Santa Rosa-Cortes Ridge and Slope	23
Northern Santa Rosa-Cortes Ridge and Slope	13

Figure III.B-1 Map of Southern California Bight showing all of the High Density Sampling Areas and Low Density Sampling Areas.

are more completely analyzed. Because of these findings, depth similarities were emphasized when looking for the similarities within and between areas.

The generalizations were based upon the five or six most numerically abundant and frequently collected species. Although many species were often both numerically abundant and frequently collected, there were enough differences so that a list of species of about ten or more were produced. When the report indicated a species appeared to be abundant or peculiar to a region through direct inspection of the samples or from the bottom photographs, it was included in the list.

These tables were generated from two sets of data: 1) the HDSA assemblages reported by Jones and Fauchald, and 2) raw data from the sampling program. Jones and Fauchald divided the HDSA into assemblages through direct inspection of the samples and data generated from their analyses and by cluster analysis. The assemblages defined by direct inspection were broader in areal extent and far less patchy as comparison of Figure III.B-2 (direct inspection) and Figure III.B-3 (cluster analyses) indicates. For this reason, the assemblages derived from direct inspection of the HDSA data were used. Two exceptions to this were the Santa Catalina Island HDSA and Santa Cruz Island HDSA in which several assemblages were combined.

During the study, benthic samples were obtained from 710 stations. Several more stations were sampled but because of rocky bottoms samples could not be obtained. Of these, only about 443 were in the HDSA, leaving a significant amount of data (approximately 267 stations) and a large area not reported. To utilize these data, a computer program was run for 11 areas (Figure III.B-1) ranking the species in order of abundance and frequency. The number of individuals and wet weight biomass of the major taxonomic groups data were also examined. The 11 areas were chosen visually and cluster analyses were run to see if any assemblages were correlated with depth. This was found to be insignificant; however, no direct inspection of the data was made to divide the area by assemblages as was done on the HDSA. Because of this, there was no separation of assemblage by depth. All data in an area were used. The density of the stations in the sampling grid was spaced father apart than the HDSA, although they were closer together than many published papers on marine benthos investigations. No species were listed from the bottom photographs taken during the sampling. (SAI-Scientific Applications Inc. - 1977).

Jones and Fauchald (1977) worked out a rapid identification method (RIP) during the study to deal with the large number of stations.

An expert of each taxomonic group was given a limited amount of time (10 minutes) to examine a sorted sample of his particular taxomonic group speciality. During this time, he identified and counted as many

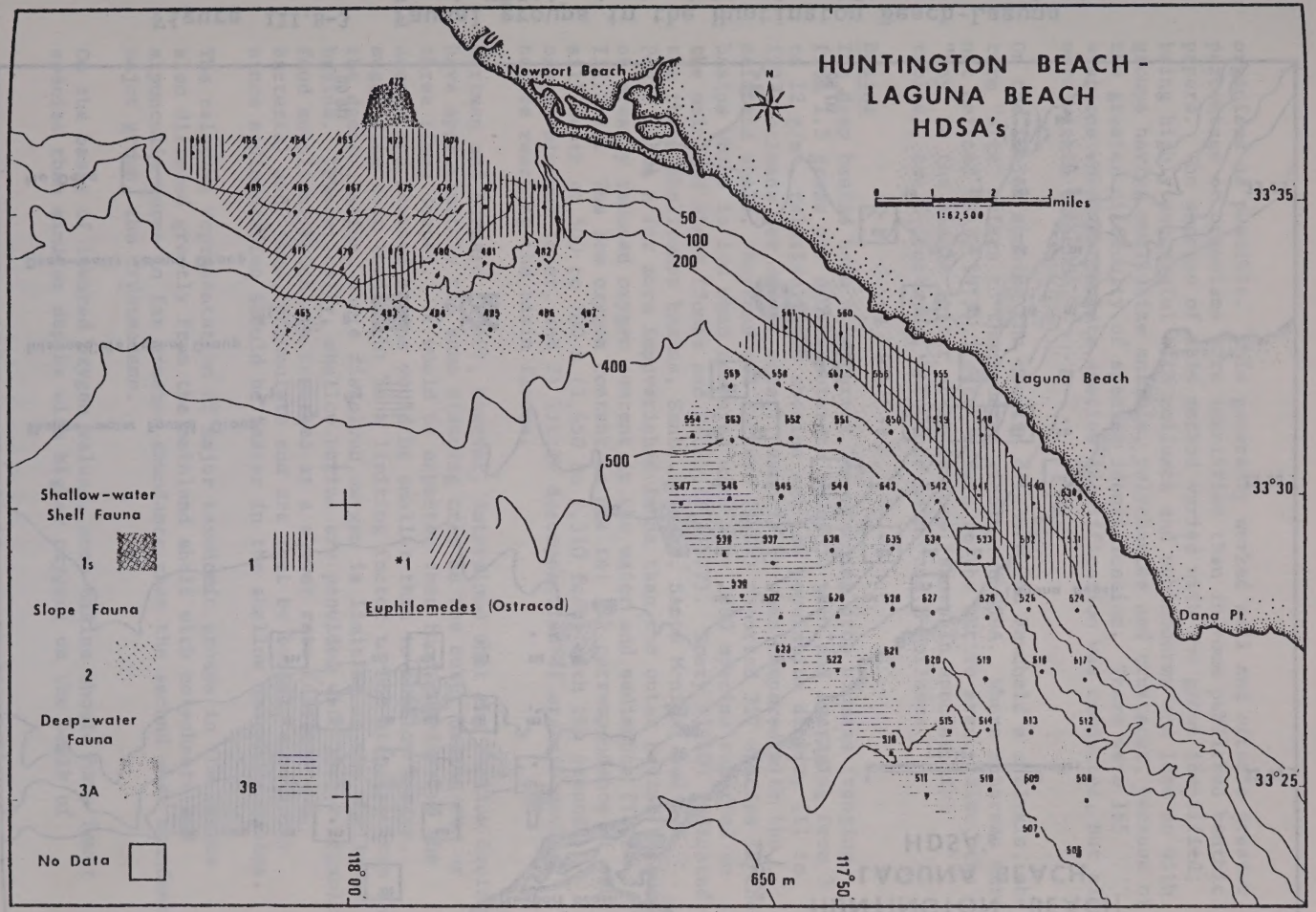


Figure III.B-2 Faunal associations in the Huntington Beach-Laguna Beach HDSA's derived by direct inspection.

Source: Jones and Fauchald (1977).

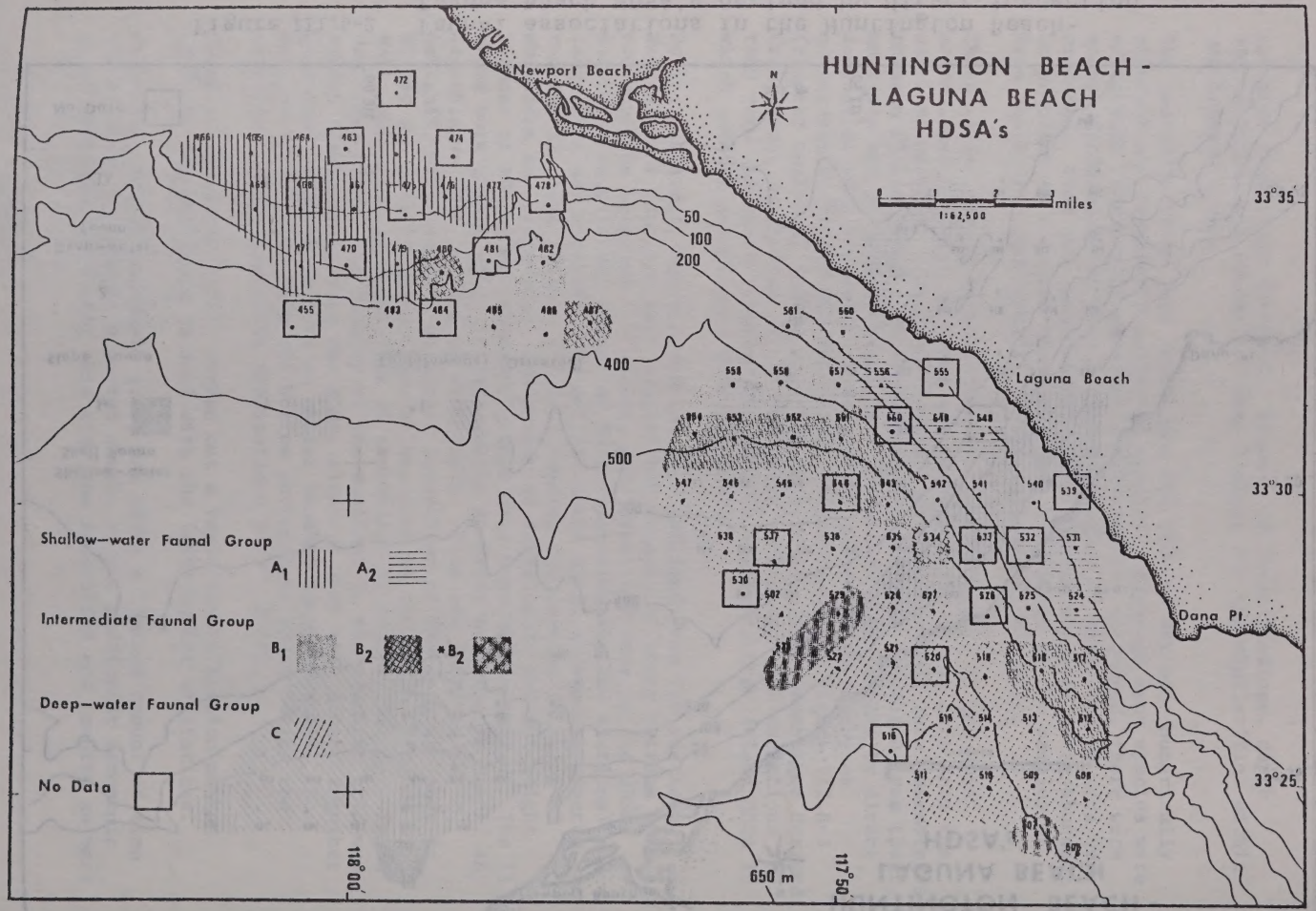


Figure III.B-3 Faunal groups in the Huntington Beach-Laguna Beach HDSA's derived by classification analysis.

Source: Jones and Fauchald (1977).

organisms as possible. This generally worked well and often a greater percentage of organisms were identified than in some published benthic papers. The success of this method varied with the group identified, being highly successful with molluscs and echinoderms and less so with groups having small-size animals, polychaetes and crustacea, because of the greater difficulty of species identification. There were 165 stations where a complete species identification was conducted, but all were within the HDSA.

On the tables showing the results of Jones and Fauchald's analysis, the term "site" refers to the subarea within the HSDA. Where subareas were not defined (SAI, 1977), "site" refers to the entire area. Also, the "key" to the single letter abbreviations (shown in species list tables), are C-Crustacea, E-Echnodermata, and M-Mollusca.

Basins

The deep basins have a uniformly low standing crop biomass (ranging from 1.5 grams per square meter to about 50 g/m^2 and averaging from 3 to 12 g/m^2, relatively few species and low population density (11 to 120 specimens per square meter), especially when compared with the mainland shelf. Hartman and Barnard (1960) reported 317 species in the basins which is low when compared with over 1700 species reported on the mainland shelf (Jones and Fauchald, 1977). Emery (1960) indicated the three shallowest basins, Santa Barbara, Santa Monica, and San Pedro, have a far more impoverished fauna than the outer basins because of greatly reduced oxygen content in the water and sediments (Table III.B-1). The low oxygen content is due to: 1) correspondence of the sill depth at 500 to 700 m (1,650 to 2,310 feet) with the oceanic oxygen minimum layer, and 2) little decomposition of organic matter before reaching the basin floors.

Hartman and Barnard (1960), however, determined that the shallow basins have approximately the same standing crop as the outer basins two or three times deeper. It would be expected that food supplies to the deeper and seaward basins would be smaller than to shallow basins, suggesting that food might be a limiting factor to the standing crop in the deeper basins, while dissolved oxygen is limiting in the shallower basins. Theoretically, shallow basins are provided with larger organic food supplies, which are reworked at a slower rate (discounting bacteria) and, thus, accumulate and are lost by burial, especially since sedimentation should be faster in the shallow nearshore basins.

The relative representation of major taxonomic groups in the basins also differed greatly from the mainland shelf with polychaete and sipunculid worms in far greater abundance than the second most abundant major group, the crustaceans.

On the basis of lowered oxygen values, some basins should have fewer species than similar depths with higher oxygen; on the basis of

Table III.B-1

PHYSICAL AND BIOLOGICAL DATA FROM THE BASINS OFF SOUTHERN CALIFORNIA

Basin	Depths		Bottom Temp (°C)	Bottom Dissolved Oxygen (mg/L)	No. of Benthic Samples	No. of Living Species	Mean Standing Crop (g/sq m)	Density (no./sq m)
	Sill (m)	Bottom (m)						
Santa Barbara	475	627	6.3	0-0.3[a]	5	24	2.8 (42.0)[b]	50
Santa Monica	737	938	5.0	0-0.3[a]	19	24	4.4	11
San Pedro	737	912	5.1	0.2	70	115	5.5	31
Santa Cruz	1,085	1,966	4.2	0.8	9	55	3.2	61
San Nicolas	1,106	1,833	3.7	0.5	11	90	5.5	121
Santa Catalina	974	1,357	4.0	0.4	11	119	8.3	123
San Clemente	1,815	2,107	2.6	1.3	6	53	1.5	34
East Cortes	1,415	1,979	3.1	0.9	3	36	6.1	66
Tanner	1,165	1,551	3.8	0.6	6	71	10.0	89
West Cortes	1,362	1,769	3.4	0.8	4	42	4.2	66
Velero	1,902	2,571	2.5	2.0	2	20	4.2	43
Long	1,697	1,938	2.7	1.4	3	54	12.0 (49.7)[c]	98

Source: After Hartman and Barnard 1960. Bottom dissolved oxygen and temperature from Emery 1960.

[a]Water in the extreme bottoms is anoxic.
[b]With heavy molluscs.
[c]With one large echiuroid.

distance from shore and depth, the inshore basins should have a higher food supply and more numerous species than deeper offshore basins. It would appear that oxygen is the more critical limiting factor, since the three shallower basins with higher food supply have in two cases far fewer species than almost all other deeper basins; and in the case of the much better sampled San Pedro Basin with its 115 species, only slightly fewer than the deeper and poorly sampled Santa Catalina Basin with 119 species (Table III.B-1). The greater number of samples taken from San Pedro Bay favored the collection of a greater number of species.

About half the species occupying basin floors normally live on the mainland shelf in depths of 120 m (feet) or less. The three shallower nearshore basins had a higher percentage of shelf species (68 percent) than the three deeper offshore basins (46 percent). Twenty-four species were common to five or more of the ten basins considered. The polychaete worms *Aricidea uschakovi* and *Phyllochaetopterus limicolus* were common in ten basins.

Hartman and Barnard defined two major communities based upon principal and dominant species. These communities separate the inner shallow San Pedro and Santa Monica Basins from the outer basins whose *Aricidea-Tharyx* community was divided into three Facies (Table III.B-2). Santa Barbara and Velero Basins were considered too poorly known for such community definition treatment.

Table III.B-2

COMMUNITIES OF SOUTHERN CALIFORNIA DEEP WATER BASINS

Phyllochaetopterus limicolus-Protis pacifica-Cyclopecten zephyrus
San Pedro and Santa Monica Basins
Aricidea uschakovi-Tharyx tesselata
Santa Cruz, Long, Tanner Basins
Facies *Praxillella* spp.
Santa Catalina Basin
Facies "sipunculids"
San Nicolas Basin
Facies *Ceratocephala loveni pacifica*
West Cortes, San Clemente, East Cortes Basins

Source: (Hartman and Barnard, 1969).

Table III.B-3

DOMINANT BENTHIC INVERTEBRATES OF THE BASIN FAUNA (Z> 1,600 m; $\bar{x}$ = 1816 m) Assemblage at Santa Rosa Ridge-Santa Cruz Basin High Density Sampling Area

		Abundance Value Mean No.				
		Rank	Site	Rank	Value	Percent
Echinodermata						
[a]*Ophiura leptoctenia*	brittle star	2	3.4	2	9/11	81.8
Crustacea						
Eudorella pacifica	cumacea	5	0.4	8	2/11	18.2
Heterophoxus oculatus	amphipod	6	0.4	4	4/11	36.4
Mollusca						
[a]*Tindaria kennerlyi*	clam	1	5.6	1	11/11	100.0
Mysella compressa	clam	4	0.5	5	4/11	36.4
Polychaeta						
Rhodine bitorquata		3	2.4	3	9/11	81.8

Source: (Jones and Fauchald, 1977).

[a]The characteristic species of the assemblage.

Jones and Fauchald (1977) sampled Santa Cruz Basin (see Table III.B-3 for a reduced species list), and reported as dominants only two species (*Ophiura leptoctemia* and *Heterophoxus oculatus*) which were also collected by Hartman and Barnard (1958 and 1960).

The number of individuals in a sample was greatly reduced compared to more shallow areas. The most numerically dominant and frequently encountered species from San Pedro, Santa Monica, Santa Catalina, and San Nicolas Basins are shown in Tables III.B-4 through III.B-7 (SAI, 1977) and Santa Cruz Basin in Table III.B-3 (Jones and Fauchald 1977). Although the two outer basins were sampled at only five stations, some conclusions about most common species might be hypothesized. No widely distributed species were found. None were collected from all five basins and only two of the most frequently occurring species were collected in more than two basins, the bivalve *Tomburchus redondoensis* (San Pedro, Santa Monica, and Santa Cruz Basins) and the polychaete *Spiophanes* sp. (San Pedro, Santa Monica, and Santa Cruz).

Table III.B-4

DOMINANT BENTHIC INVERTEBRATES OF SAN PEDRO BASIN
($\bar{Z}$ = 622 m to 888 m; $\bar{x}$ = 798 m)

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Eclysippe trilobatus Polychaeta	1	4.9	2	5/12	41.7
Mitrella permodesta M-snail	2	2.7	1	7/12	58.3
Aricidea complex Polychaeta	3	1.4	3	4/12	33.3
Tomburchus redondoensis M-bivalve	4	0.4	4	2/12	16.7
Cadulus californicus M-	5	0.3	4	2/12	16.7
Liljeborgia cota C-	5	0.3	4	2/12	16.7
[a]*Phyllochaetopterus* sp.	-	(4.9)	-	(8/12)	(66.7)
Spiophanes sp.	-	(1.9)	-	(5/12)	(41.7)

Source: SAI (1977).

[a]Possible polyspecific species with high rankings.

Table III.B-5

DOMINANT BENTHIC INVERTEBRATES OF SANTA MONICA BASIN
($\tilde{z}$ = 584 m to 888 m; $\bar{x}$ = 657 m)

	Abundance		Frequency	
	Rank	Value Mean No./ Site	Rank	Value	Percent
Tomburchus redondoensis M-bivalve	1	1.3	1	2/8	25.0
Cadulus californicus M-	2	0.8	-	1/8	12.5
Amphipholis squamata E-brittle star	3	0.7	1	2/8	25.0
Ilyarachna acornia C	4	0.5	-	1/8	12.5
Liljeborgia cota C	4	0.5	-	1/8	12.5
Amphipholis pugetana E-brittle star	4	0.5	-	1/8	12.5
[a]*Spiophanes* sp. Polychaete	-	(2.4)	-	(3/8)	(37.5)
Phyllochoetopterus sp. Polychaete	-	(1.4)	-	(3/8)	(37.5)
Cadulus sp. M-	-	(1.2)	-	(3/8)	(37.5)
Caprellidae unidentified C-amphipod	-	(1.2)	-	(1/8)	(12.5)

Source: SAI (1977).

Table III.B-6

PRINCIPAL BENTHIC INVERTEBRATES OF THE NORTHERN PORTION OF SANTA CATALINA BASIN
($\bar{z}$ = 1139 m to 1309 m; $\bar{x}$ = 1215 m)

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Ophiura leptoctenia E	1	2.0	1	3/5	60.0
Tauberia oculata Polychaeta	2	1.8	1	3/5	60.0
Maldane cristata Polychaeta	3	1.6	1	3/5	60.0
Ophiophthalmus normani E-	4	0.7	4	2/5	40.0
Pista near *fasciata*	5	0.6	4	2/5	40.0
Tindoria californica M-	-	0.4	4	2/5	40.0
Tindaria kennerlyi M	-	0.4	4	2/5	40.0
Liljeborgia cota C	-	0.5	4	2/5	40.0
[a]*Cirratulidae*, unidifiable Polychaeta	-	(1.4)		(2/5)	(40.0)
Chaetoderma sp. M-*Aplacophora*	-	(1.2)		(4/5)	(80.0)

Source: SAI (1977).

Table III.B-7

PRINCIPAL BENTHIC INVERTEBRATES OF THE CENTRAL PORTIONS OF SAN NICOLAS BASIN
(R = 1544 m to 1764 m; $\bar{X}$ = 1712 m)

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Melinnampharete gracilis Polychaete	1	1.0	1	4/5	80.0
Thyasira flexuosa M	1	1.0		1/5	20.0
Myriochele near *gracilis* Polychaeta	3	0.4	2	2/5	40.0
[a]Cirratulidae, unidentifiable Polychaete		(1.4)		(3/5)	(60.0)
Chaetoderma sp. M-*Aplacophora*	-	(2.0)	-	(1/5)	(20.0)
Golfingia sp.	-	(6.8)	-	(4/5)	(80.0)

Source: SAI (1977).

[a]Possible polyspecific species with high ranking.

The inner basins, as would be expected, had the most similarity, being characterized by the polychaete worms *Phyllochaetopterus* sp. and *Spiophanes* sp. (38 to 67 percent frequency) and to a far lesser extent by the molluscs *Tomburchus rodondoensis* and *Cadulus californias* Tables III.B-3, and III.B-4).

The echinoderm *Ophiura leptoctenia* and the apolocophoran mollusc *Chaetoderma* sp. were most frequently encountered in the Santa Catalina Basin while the polychaete *Melinnampharete gracilis* and the sipunculid worm *Golfingia* sp. were the most frequent at San Nicolas Basin (Table III.B-5 and III.B-6).

Comparison between these data and those of Hartman and Barnard (1960) points out several differences. Although Hartman and Barnard reported the worms *Phyllochaetopterus limicolus* and *Aricidea uschakovi* to be common to ten basins, *Poyllochaetopterus* sp. (possibly the same species, but not identifiable to this level by the RIP Method, used by Jones and co-workers) was collected or important only in the inner basins during the SAI study.

Aricidea sp. was collected but as a different species (*A. complex* and *A. guadrilauata*) during the SAI study in Santa Catalina and Santa Rosa Basins in addition to the inner basins.

Protis pacifica and *Cycloperten zephyrus*, reported by Hartman and Barnard to be characteristic of the inner basins, were not collected at all in these areas during the SAI Study.

Apparently the population of a given species is so sparse that there is a low probability of taking even the more common species in every or even the majority of samples. Under these conditions, it is difficult to characterize associations based on dominant species.

Slopes

Jones and Fauchald (1977) sampled two mainland slopes, at Huntington-Laguna Beach and at Point Dume, an island which, although they are essentially shelves, had several stations which may have been close to slope in nature and location (San Miguel) and the slope from the Santa Rosa-Cortes Ridge into the Santa Cruz Basin (Tables III.B-8 through 11).

Examination of data from Huntington-Laguna Beach and Point Dume, (Tables III.B-8 and III.B-9) indicates the most frequently encountered benthic species was the ice cream cone worm *Pectinaria californiensis*. Other species having wide distributions, based on frequency of occurrence are the shelless aplocophoran *Limifossor fratula*, the polychaete *Prionospio cirrifera*, and, based upon abundance, the bamboo worm *Maldane sarsi*. The amphipods *Heterophoxus oculatus* and *Ampelisca Macroephala* and the bamboo worm *Maldane glebifex* might be added to this

Table III.B-8

DOMINANT BENTHIC INVERTEBRATES OF THE SLOPE FAUNA
(161 m to 520 m) Assemblage at Huntington-Laguna Beach HDSA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
[b]*Allocentrotus fragilis* sea urchin	-	-	-	-	-
[b]*Amphiodia urtica* brittle star	5	1.1	-	1/13	7.7
Crustacea					
Ampelisca macrocephala amphipod	3	1.4	4	4/13	30.8
Mollusca					
Mysella tumida clam	6	1.0	-	1/13	7.7
[a]*Limifossor fratula* shelless aplacophora	13	0.6	3	6/13	54.5
[a]*Chaetoderma* spp. shelless aplacophora					
[b]*Cyclocardia ventricossa* clam	15	0.5	8	3/13	23.1
[b]*Bittium paganicum* snail	-	-	-	-	-
Polychaeta					
[a]*Pectinaria californiensis*	1	3.2	1	12/13	92.3
Maldane sarsi	2	2.1	22	2/13	15.4
Lumbrineris sp.	4	1.4	11	3/13	23.1
Paraprionospio pinnata	7	0.9	2	9/13	69.2
Mediomastus californiensis	11	0.7	6	4/13	30.8
Prionospio cirrifera	17	0.5	7	4/13	30.8

Source: Jones and Fauchald, 1977

[a]The characteristic species of the zone.
[b]Common by visual inspection.

Table III.B-9

DOMINANT BENTHIC INVERTEBRATES OF THE INTERMEDIATE FAUNAL (303 m to 481 m) Assemblage at Point Dume High Density Sampling Area

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
Brisaster latifrons sea urchin	10	0.6	5	4/10	40.0
[a]*Allocentrotus fragilis* sea urchin	-	-	-	-	-
[a]*Brissopsis pacifica* sea urchin	-	-	-	-	-
Crustacea					
Heterophoxus oculatus amphipod	4	1.4	1	6/10	60.0
Eudorella pacifica cumacea	13	0.4	7	4/10	40.0
Ampelisca macrocephala amphipod	9	0.6	9	3/10	30.0
Mollusca					
Cyclocardia ventricosa bivalve	7	0.8	6	4/10	40.0
Limifossor fratula aplacophora	8	0.8	8	4/10	40.0
Chaetoderma spp. aplacophora					
Polychaeta					
Maldane glebifex bamboo worm	1	7.7	2	6/10	60.0
Maldane sarsi bamboo worm	2	4.7	16	2/10	20.0
Chloeia pinnata	3	2.1	11	3/10	30.0
Pectinaria californiensis	5	1.2	4	6/10	60.0
Paraprionospio pinnata	6	1.0	3	6/10	60.0

Source: Jones and Fauchald, 1977.

[a]Common by visual inspection.

Table III.B-10

(A) DOMINANT BENTHIC INVERTEBRATES OF THE INTERMEDIATE-WATER (500 m to 600 m) ASSEMBLAGE AT SANTA ROSA RIDGE-SANTA CRUZ BASIN HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata *Amphipholis pugetana* brittle star	2	0.5	-	1/2	50.0
Mollusca *Huxleyia minuta* clam	1	1.0	-	1/2	50.0
?*Clavopora occidentalis*	3	0.5	-	1/2	50.0
(B) Slope Fauna 600-1600 m $\bar{x}$ = 1200 m					
Echinodermata *Amphipholis squamata* brittle star	3	1.3	15	1/11	9.1
Amphipholis pugetana brittle star	6	-	14	1/11	9.1
Crustacea *Byblis tannerensis* amphipod	1	10.0	8	2/11	18.2
Ampelisca macrocephala amphipod	2	5.8	4	3/11	27.3
Heterophoxus oculatus amphipod	12	0.3	5	3/11	27.3
Eudorella pacifica cumacea	13	0.2	9	2/11	18.2
Eurycope californiensis isopoda	11	0.3	10	2/11	-
Mollusca [a]*Tomburchus redondoensis* clam	8	0.7	2	6/11	54.5
Adontorhina cyclia clam	5	0.7	3	4/11	36.4
Polychaeta *Spiochaetopterus costarum*	4	1.0	1	7/11	63.6

Source: (Jones and Fauchald, 1977).

[a]Characteristic species of the area.

Table III.B-11

DOMINANT BENTHIC INVERTEBRATES OF THE DEEP-WATER ($\bar{z}$ = 200 m to 500 m; $\bar{x}$ = 239 m) ASSEMBLAGE AT SAN MIGUEL ISLAND HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
[b]*Allocentrotus fragilis* urchin		-	-	-	-
[b]*Brissopsis pacifica* urchin		-	-	-	-
Above species seldom collected shallower than 200 m					
Amphiodia urtica brittle star	1	10.6	5	3/5	60.0
Crustacea					
Ilyarachna profunda isopod					
Ampelisca macrocephala amphipod	6	1.8	22	1/5	20.0
Haliophasma geminata isopod	9	1.4	7	3/5	60.0
Byblis veleronis amphipod	10	1.2	6	3/5	60.0
Paraphoxus bicuspidatus amphipod	12	1.2	10	3/5	60.0
Ampelisca pacifica amphipod	16	0.8	4	3/5	60.0
Ampeliscidae amphipod					
Phoxocephalidae amphipod					
Mollusca					
Parvilucina tenuisculpta clam	2	8.0	3	4/5	80.0
[a]*Tellina carpenteri* clam	3	3.2	1	5/5	100.0
[b]*Tindaria californica* clam		Only at deepest stations			
Polychaeta					
Lumbrineris sp.	4	2.4	9	3/5	60.0
Maldane glebifex	7	1.6	2	4/5	80.0
Laonice cirrata	15	1.0	8	3/5	60.0
Scalibregma sp.	14	1.2	12	3/5	60.0
Chloeia pinnata	5	2.0	30	1/5	20.0

Source: (Jones and Fauchald, 1977).

[b]Common by direct inspection.

list but appeared to be somewhat more typical of the Point Dume Area than of the Huntington-Laguna Beach area. Those fairly frequent by observation, including camera data, are the echinoderms *Allocentrotus fragilis* and *Brissopsis pacifica*. Both HDSAs illustrate the expected decrease in species (and individuals) with depth and distance from shore. The mean number of species decreased in the HDSA by 50 percent (49 to 24) and by a factor of 4 (66 to 16) from the shallow water fauna and slope fauna at the Huntington-Laguna Beach and Point Dume HDSA, respectively. The same trend was evident in the mean number of individuals which decreased by a factor of from 5 and 9. A mean wet weight standing crop difference between the mainland shelf and slope were not evident, although an "atypical" sample or samples could have weighted the deeper areas somewhat high (Jones and Fauchald, 1977).

The slope fauna of the Santa Cruz Basin was most characterized in terms of frequency of occurrence, by the polychaete *Spiochaetopterus costarum* and the bivalve *Tomburchus redondoensis*, both collected at 63.6 percent of the stations. These were the only species collected at more than 50 percent of the stations (Table III.B-10).

Jones and Fauchald reported in their narrative that the bivalve *Adontorhina cyclia* (36.4 percent frequency) was also somewhat characteristic of the area. Based upon numerical abundance, the amphipods *Byblis tannerensis*, and the familiar *Amphipholis squamata* might be added to the list, but because of their low frequencies this statement may be somewhat tenuous. As with the mainland shelf, the number of species on the Santa Cruz Basin slope decreased (by a factor of 3) as did the number of individuals (by a factor of 4) from the shallow water fauna.

The slope regions were not separated in the gross area computer program; therefore, cannot be discussed here.

An examination of a bathymetric chart reveals that Jones and Fauchald's deep-water assemblage (Table III.B-11) is located on the actual topographic slope of the San Miguel Island shelf and should be representative of its slope. Based upon frequency, the bivalve *Tellina carpenteri* (100 percent frequency) followed by the omnipresent clam *Parvilucina tenuisculpta* and the bamboo worm *Maldane glebifex* (both 60 percent frequency) are the most common representatives. In addition to the above three species, there were eight more occurring in over 50 percent of the samples, indicating that in spite of the small number of stations, these species may be representative of the area. Based upon abundance, the brittle star *Amphiodia urtica* and the polychaetes *Lumbrineris* sp. might be added to this list.

Probably because of the differences in depth and location, no species are well represented in all areas although the amphipod *Ampleisca macrocephala* comes close.

Submarine Canyons

The canyons extending from the coastline to the deep basins contain unique and varied fauna (Hartman, 1963). Canyon habitats are subject to considerable fluctuations in environmental conditions because they serve as natural channels for shoreward movements of upwelling waters and organisms and for downward transport of runoff, sand, and debris. These processes result in widely varying conditions, to which the indigenous organisms must adjust.

Hartman (1963) surveyed the 13 large canyons off Southern California (Figure III.B-4). The principal species of the canyons differed from those of the mainland shelf only meters away; species composition reflected bottom sediment size and depth. No communities based on dominant species were defined. Hartman summarized some conclusions respecting the fauna of the canyons:

(1) Each canyon is found to support a richly diversified fauna, high in specific entities, with as many as 262 species in a longshore (Newport) canyon. (See Table III.B-12).
(2) The largest numbers of species in a canyon occur in shallowest, or shelf depths, and they are members of the shelf or slope fauna. There is a gradual decline in numbers of species (though not necessarily specimens) with depth, but there are deviations from this principle, perhaps partly due to factors other than depth.
(3) Most species occur as single or few specimens in a sample.
(4) Many species are represented by peak or high numbers in one or a few samples, from widely dispersed places; such peak numbers may be correlated with optimum conditions for the species, with gregariousness, or with recent spat-falls of individual species, but not usually with food concentrations.
(5) The replacement of species from one canyon to the next is such that from 30 to 60 percent are different. The differences may be partly correlated with latitude, with change in sediments, with distance from shore, or with other, still unknown factors, concerned with the biology of specific entities.
(6) Replacement of species within a canyon with increasing depth is also abrupt, so that more than 50 percent of the species may differ from one depth class to the next.

Santa Rosa-Cortes Ridge and Other Mid-Depth Areas

This division of the narrative is a somewhat broadly defined category which has characteristics of several other topographic and areal categories, but is unique because: 1) each area is somewhat geographically removed from land and the assumed influence of these bodies, 2) with the exception of two areas (Santa Cruz Basin of comparable depth and Santa Catalina Island HDSA) none of these areas

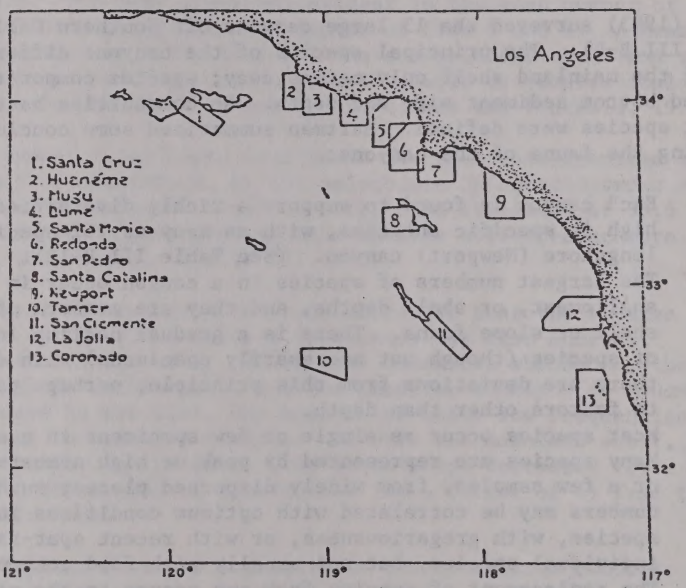


Figure III.B-4 Index map showing the locations of the thirteen submarine canyons biologically sampled.

Source: Hartman (1963).

Table III.B-12

RELATIVE COMPOSITION OF CANYON INVERTEBRATES[a]

Canyon	No. of Samples	Percent of Identified Species: Poly-Chaetes	Crusta-cears	Molluscs	Echino-derms	Others	No. of Species Identified
Hueneme	14	56.6	14.5	14.5	4.4	10.1	159
Mugu	10	47.1	28.1	12.8	5.8	6.2	242
Dume	10	58.2	17.6	13.2	6.6	4.4	91
Santa Monica	15	69.4	8.2	9.4	6.5	6.5	170
Redondo	13	63.1	7.7	18.4	5.9	4.8	168
San Pedro Sea Valley	15	67.9	5.2	11.8	8.0	7.1	212
Newport	16	56.9	14.5	16.4	5.3	6.9	262
Mean		59.9	13.7	13.8	6.1	6.6	(149)

[a]From SCCWRP (1973).

were HDSA subjected to detailed analyses which determined assemblage divisions based upon the entire macro-invertebrate population. Rather, they were intuitively selected according to location similarities sometimes having similar depths. Only the numerically dominant and most frequently occurring species were determined for the entire area, and 3) most stations were within a depth of about 200 m to 500 m (600 to 6,650 feet) (except for Santa Rosa-Cortes Ridge, which had a far greater depth range and will be considered separately below), with the majority of these between 250 m and 350 m (825 to 1,115 feet).

The areas considered in this scheme were the Santa Barbara Island region, the Catalina Island HDSA, Santa Rosa-Cortes Ridge North, Santa Rosa-Cortes Ridge South, and the shallow and intermediate zones of the Santa Rosa-Ridge Santa Cruz Basin HDSA. The principal species of these areas are shown in Tables III.B-13 through III.B-17 and III.B-10 A respectively and their depth ranges are shown below:

	Depth Range	Mean
Santa Barbara Island Area	140-481 m	292 m
Catalina Island HDSA A[a]	222-407 m	335 m
B	227-461 m	342 m
C		453 m
Santa Rosa-Cortes Ridge, North	82-976 m	638 m
Santa Rosa-Cortes Ridge, South	107-1054 m	434 m
Santa Rosa Ridge-Santa Cruz Basin-Shallow HDSA		234 m
Santa Rosa Ridge-Santa Cruz Basin Intermediate HDSA	500-600 m	

[a]Since there were no faunal assemblages apparent by visual inspection, the cluster analyses from this area were used.

Considering the Santa Barbara Island area and Catalina Island HDSA together, there is little evidence for any frequently occurring species, particularly of the same magnitude as that of the coastal shelf areas presented below. The only species approaching a representative species for these areas are brittle stars of the genus *Amphipholis* spp. *Amphipholis squamata* was collected at 47.2 percent of the stations (36) of these two areas and *Amphipholis pugetana* was collected at 38.9 percent.

Examination of Table III.B-13 indicates that, while no species was very frequent on the Santa Catalina shelf and slope (63.6 percent maximum) eight species occurred at more than 50 percent of the stations. Four species were incompletely identified and may represent a greater number of species than are represented in the table. In spite of these numbers, the area around Santa Barbara Island is not well characterized by dominant species. The cluster analyses used to characterize Catalina Island assemblages did a good job of selecting discrete faunal groups whose principal species have an abundance and frequency. It

Table III.B-13

PRINCIPAL BENTHIC INVERTEBRATES OF SHELF AND SLOPE AREA AROUND SANTA BARBARA ISLAND
($\bar{z}$ = 140 m to 481 m; $\bar{x}$ = 292 m)

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Chloeia pinnata Polychaeta	1	5.9	-	2/11	18.2
Amphipholis squamata E-brittle star	2	5.4	1	7/11	63.6
Amphipholis pugetana E-brittle star	3	3.3	2	6/11	54.5
Amphiodia urtica E-brittle star	4	1.4	2	6/11	54.5
Adontorhina cyclia M-	4	1.4	-	2/11	18.2
Bathymedon pumilus C-	6	1.2	-	2/11	18.2
Terebellides stroemii Polychaeta	-	0.6	2	6/11	54.5
Laonice cirrata Polychaeta	-	0.4	5	4/11	36.4
Hanleya hanleyi M	-	0.6	5	4/11	36.4
Ampelisca pacifica C-amphipod	-	0.7	5	4/11	36.4
Aoroides columbiae C-amphipod	-	0.6	5	4/11	36.4
[a]Cirratulidae unidentified Polychaeta	-	(3.1)	-	(4/11)	(36.4)
Glycera sp. Polychaeta	-	(1.2)	-	(6/11)	(54.5)
Lanassa sp. Polychaeta	-	(0.5)	-	(6/11)	(54.5
Ophiuroidea E-brittle star	-	(2.4)	-	-	(54.5)
Amphiuridae, unidentified E	-	(1.2)	-	(6/11)	(54.5)

Source: SAI (1976).

Table III.B-14

DOMINANT BENTHIC INVERTEBRATES OF SANTA CATALINA ISLAND
HDSA DERIVED FROM CLASSIFICATION ANALYSIS

Group A ($\tilde{z}$ 222 m to 407 m; $\bar{x}$ = 335 m)

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Lumbrineris sp.	1	2.7	1	6/8	75
Amphiodia urtica	2	1.2	1	6/8	75
Ilyarachna acarina	3	0.9			
Megacreneila columbiana	4	0.6	4	3/8	37.5
Prionospio near *malmgreni*	5	0.6	3	4/8	50
Parvelucina tenuisculpta	6	0.5	4	3/8	37.5
Ampelisca pacifica	7	0.4	4	3/8	37.5
Paraprionospio pinnata	7	0.4	4	3/8	37.5

Group B ($\tilde{z}$ = 227 m to 461 m; $\bar{x}$ = 342 m)

Euphilomedes Carcharondonta C-amphipod	1	10.7	2	6/9	66.7
Huxleyia minuta M-bivalue	2	4.2	2	6/9	66.7
Ampelisca pacifica C-amphipod	3	2.0	4	5/9	55.5
Tellina carpenteri M-bivalve	4	2.0	1	7/9	77.8
Philomedes dentata C-ostracod	5	1.9	5	4/9	44.4

Table III.B-14

CATALINA ISLAND HDSA (Cont.)

	Abundance		Frequency		
	Rank	Value Mean No./ Group	Rank	Value	Percent
Group C ($\bar{z}\ \bar{x}$ = 453 m)					
Dacroydium sp.	1	25.7	4	3/4	75
Adontorhina cyclia	2	6.2	1	4/4	100
Maldane glebifex	3	5.7	4	3/4	75
Tomburchus redondoensis	4	2.7	1	4/4	100
Amphipholis pugetana	5	1.7	4	3/4	75
Amphipholis squamata	6	1.7	1	4/4	100
Heterophoxus oculatus	7	1.5	4	3/4	75
Pardisynopia synopiae	7	1.5	4	3/4	75
Pseudomma berkeleyi	10	0.7	4	3/4	75
Thyasira sp. A	13	0.7	4	3/4	75
Group D ($\bar{z}\ \bar{x}$ = 537 m)					
Tomburchus redondoensis	1	4.7	1	5/6	83.3
Dacrydium sp.	2	1.8	4	3/6	50.0
Adontorhina cyclia	3	1.2	1	5/6	83.3
Terebellides stroemii	4	1.2	1	5/6	83.3
Eudorella pacifica	5	0.5	-	2/6	33.3
?*Golfingia bulbosa*	5	0.5	-	2/6	33.3
Mitrella permodesta	5	0.5	-	2/6	33.3

Table III.B-15

PRINCIPAL BENTHIC INVERTEBRATES ON
ON NORTH SANTA ROSA - CORTES RIDGE AND SLOPE
($\tilde{z}$ = 82 m to 976 m; $\bar{x}$ = 638 m)[a]

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Myriochele near *gracilis* Polychaeta	1	9.0	2	5/13	38.5
Ampelisca catalinensis C-amphipod	2	3.6	2	5/13	38.5
Ampelisca macrocephala C-Amphipod	3	3.4	-	2/13	15.4
Onuphis near *nebulosa* Polychaeta	4	1.8	2	5/13	38.5
Owenia collaris Polychaeta	5	1.7	-	2/13	15.4
Huxleyia minuta M-bivalve	5	1.7	-	2/13	15.4
Lumbrineris sp. Polychaeta	-	1.1	1	7/13	53.8
Praxillella affinis pacifica Polychaeta	-	0.8	5	4/13	30.8
Adontorhina cyclia M	-	0.4	5	4/13	30.8
Tellina carpenteri M-bivalve	7	1.4	5	4/13	30.8
Liljeborgia cota C-	-	0.3	5	4/13	30.8
[b]*Photis* spp. C-amphipod	-	(4.9)	-	(5/13)	(38.5)

[a]Number of stations less than 250 m = 1.
Number of stations between 250 m and 500 m = 4.
Number of stations between 500 m and 1,000 m = 8.

Table III.B-16

PRINCIPAL BENTHIC INVERTEBRATES OF
SOUTHERN SANTA ROSA - CORTES RIDGE AND SLOPE
($\bar{Z}$ = 107 m to 1,054 m $\bar{x}$ = 434 m)[a]

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Amphipholis squamata E-brittle star	1	4.2	2	10/23	43.5
Amphipholis pugetana E-brittle star	2	2.9	1	12/23	52.2
Adontorhina cyclia M-	3	1.5		5/23	21.7
Byblis veleronis C-amphipod	4	1.1	6	6/23	26.1
Aricidea complex Polychaeta	5	0.9	3	8/23	34.8
Laonice cirrata Polychaeta	5	0.9	-	5/23	21.7
Chloeia pinnata Polychaeta	5	0.9	-	4/23	17.4
Ampelisca catalinensis C-amphipod	5	0.9	-	3/23	13.0
Tellina carpenteri M-bivalve	-	0.9	3	8/23	34.8
Urothoe varvarina C-	-	0.4	5	7/23	30.4
[a]*Amphiuridae* unidentifiable E-		(3.1)	-	(11/23)	(47.8)

Source: SAI (1976).

[a]Number of stations less than 250 m = 2.
Number of stations between 250 m and 500 m = 13.
Number of stations between 500 m and 1,000 m = 4.

Table III.B-17

DOMINANT BENTHIC INVERTEBRATES OF THE SHALLOW-WATER (234 m) ASSEMBLAGE AT SANTA ROSA RIDGE - SANTA CRUZ BASIN HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
[a]*Amphipholis squamata* brittle star	1	8.7	1	4/4	100.0
[a]*Amphipholis pugetana* brittle star	2	2.7	2	3/4	75.0
Ophiopholis bakeri brittle star	6	1.5	2	3/4	75.0
Allocentrotus fragilis sea urchin	10	1.0	2	3/4	75.0
Crustacea					
Photis lavica amphipod	7	1.5	2	3/4	75.0
Aoroides columbiae amphipod	3	2.0	2	3/4	75.0
Urothoe varvarini amphipod	5	2.0	12	2/4	50.0
Polychaeta					
Peisidice aspera polychaeta	9	1.2	2	3/4	75.0
?*Clavopora occidentalis*	4	2.0	14	1/4	25.0

Source: (Jones and Fauchald, 1977).

would be difficult, however, to characterize the entire area with a good frequently encountered or abundant species. There was a similarity between the principal species of faunal Grops A and B to those of the mainland and island shelves. The polychaete *Lumbrineris* sp., brittle star *Amphiodia urtica*, and bivalve *Parvilucina tenuisculpta* from Group A and crustaceans *Euphilomedes carcharondonta* and *Ampelisca pacifica* and bivalve *Tellina carpenteri* from Group B were frequently encountered on shelf stations.

There was a difference in the number of stations at different depths between north Santa Rosa-Santa Cortes Ridge (Table III.B-15) and south Santa Rosa-Santa Cortes Ridge (Table III.B-16) which may lead to some erroneous conclusions when comparing these two sections of the ridge.

The ratio of the shallowest stations less than 250 m (825 feet) was about the same, around 8 percent but the south ridge with 57 percent mid-depth stations, 250 m to 500 m (825 to 1,650 feet) was represented by a far greater proportion of mid-depth stations than the northern ridge with 31 percent. Conversely, the northern ridge had a far greater portion of "deep water" stations 500 m to 1,000 m (1,650 to 3,300 feet) with 61 percent than the south ridge with only 17 percent. A computer program was run using cluster analysis and depth for these areas, but was found to be insignificant at the 0.05 levels (John Wilson SAI, personal communication, 1977).

Examination of Tables III.B-15 and III.B-16 indicates there were few, if any, frequently sampled species from either area. This may indicate the areas were too broad in terms of areal extent, particularly, vertical depths or that there are in reality few species having extensive enough populations in these areas to be frequently encountered. Although the former hypothesis appears more favorable at this time, further study, either by sampling or refinement of data analyses, needs to be conducted to determine if this is so. Only one species from each area, *Amphipholis squamata* from the south ridge and *Lumbrineris* sp. from the north ridge were sampled at 50 percent or more of the stations. It is not known if *Amphipholis* spp. were present in only 23 percent of the samples of the northern ridge stations because of its greater proportion of deeper stations or because of some other factor. Species which may be distinctive of their respective areas are the polychaete *Myriochele* near *gracillis* at the northern ridge and an unidentifiable echinoderm of the family Amphuridae from the southern ridge.

On Santa Rosa-Cortes Ridge, a molluscan considered to be a living fossil was collected during the BLM Baseline study. The class Monoplacophora was considered to be extinct until the 1950's when specimens were collected from deep water areas. Until the Santa Rosa-Cortes Ridge *Neopalina* sp. specimens were collected in relatively

shallow water, this group was only known to occur in deep oceanic waters.

The horizontal distribution of this species is not known, but Rawenstam (personal communication, 1977) has indicated it appears to occur on bottoms which consist of pebbles and cobbles and its depth distribution to be around 350 to 400 m (1,155 to 1,320 feet).

When considering the Santa Rosa Ridge-Santa Cruz Basin HDSA stations, Tables III.B-10 (A) and (B) as also representative of the northern ridge, along with the other open water - mud depth stations, it is evident that only brittle stars *Amphipholis* spp. are frequently encountered at all areas considered at depths roughly between 200 m and 500 m (200 to 1,650 feet).

Island Shelves

Apparently the only study dealing with island shelves prior to the BLM study was that of Mattox (1955) and consisted of 10 samples taken from the shelf off the northwest end of Santa Catalina Island.

The BLM study had two HDSA on island shelves to the south of San Miguel Island and Santa Rosa Island. As indicated above, faunal Groups A and B of the Santa Catalina Island HDSC had apparent similarities to the island shelves with respect to principal species, but were actually far enough removed from the island and in deep enough water that they probably can just as legitimately be considered open ocean mid-depth stations. The principal species of San Miguel Island shelf are presented in Tables III.B-18, III.B-19, and possibly III.B-11. The deep water slope of San Miguel Island (Table III.B-11) was presented as it has some stations actually on the shelf. The faunal associations presented in these tables were determined by visual inspection and conformed to differences in depth. The area was characterized by relatively uniform substances, mainly coarse to fine sands, but, unlike that of the mainland shelf, the sediments were often finer in the shallow water than in deeper water offshore. A west-east pattern was also noted, with coarser sediments to the west and finer sediments to the east.

No faunal groups could be determined by visual inspection in the Santa Rosa HDSA. This was apparently due to the rather uniform depth of the stations and because the benthos was distributed according to sediment. The Santa Rosa Island HDSA was a large, irregular grid of stations adjacent to the south side of the island. The bathymetric range of this HDSA was from 26 to 479 (86 to 1,580 feet). However, most of the stations (96 percent) were in water depths of 100 (330 feet) or less. Sediment complexity characterized the area. The substances at 57 percent of the sampling locations were fine, medium or coarse sand mixed with shelly debris; at 22 percent of the area, sands and silts lacked coarser or cobbles; and at 21 percent of the area, sands and silts

Table III.B-18

DOMINANT BENTHIC INVERTEBRATES OF THE SHALLOW WATER ($\bar{z}$ = 50 m to > 100 m; x = 82 m) ASSEMBLAGE AT SAN MIGUEL ISLAND HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
Lytechinus anamesus urchin (restricted to depths of >200 m)					
Dougaloplus amphacantha brittle star	18	1.7	3	8/9	88.9
Amphipholis squamata brittle star	11	2.2	5	7/9	77.8
Crustacea					
Euphilomedes producta ostracod	2	7.0	21	5/9	55.6
Byblis veleronis amphipod	4	4.3	2	8/9	88.9
Heterophoxus oculatus amphipod	13	1.9	7	7/9	77.8
Ampeliscidae amphipod					
Phoxocephalidae amphipod					
Mollusca					
Micranellum cerebricinctum snail "characteristis of areas immediately adjacent to shores"	1	11.7	29	4/9	44.4
[a]*Amphissa undata* snail	3	4.8	6	7/9	77.8
[a]*Alvinia rosana* snail	6	3.7	16	5/9	55.6
Parvilucina tenuisculpta bivalve	10	2.3	10	6/9	66.7
Tomburchus redondoensis snail	28	1.2	34	4/9	44.4

[a]The characteristic species of the zone.

Table III.B-18 (Cont.)

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Axinopsida serricata snail	37	0.6	25	4/9	44.4
Polychaeta					
Lumbrineris sp.	5	3.9	1	9/9	100.0
Polychaete distributions changed gradually causing extreme difficulty in defining assemblages. Representatives of the following families were restricted to this zone.					
Pilargidae					
Hesionidae					
Flabelligeridae					
Trichobranchidae					

Source: (Jones and Fauchald, 1977).

[a]The characteristic species of the zone.

Table III.B-19

DOMINANT BENTHIC INVERTEBRATES OF THE INTERMEDIATE-WATER (Z = 100 m to > 200 m; $\bar{x}$ = 111 m) ASSEMBLAGE (2B) AT SAN MIGUEL ISLAND HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata	-	-	-	-	-
Lytechinus anamesus sea urchin					
Amphiodia urtica	2	6.9	2	9/10	90.0
Dougaloplus amphacantha	3	2.9	6	8/10	80.0
Crustacea					
Heterophoxus oculataus amphipod	5	2.7	2	9/10	90.0
Paraphoxus bicuspidatus amphipod	6	2.7	2	9/10	90.0
Ampelisca pacifica amphipod	10	2.1	1	10/10	100.0
Pholoe glabra amphipod	12	1.8	6	8/10	80.0
Ampeliscidae					
Phoxocephalidae					
Mollusca					
[a]*Parvilucina tenuisculpta* clam	1	10.1	6	8/10	80.0
Tomburchus redondoensis clam	8	2.2	6	8/10	80.0
Tellina carpenteri clam	20	1.0	13	6/10	60.0
Amphissa undata snail	7	2.3	6	8/10	80.0
Polychaeta					
Prionospio malmgreni	4	2.8	2	9/10	90.0
Lumbrineris sp.	8	2.2	6	8/10	80.0
Sabellidae					

Source: (Jones and Fauchald, 1976).

lacked coarser fragments of either biological or classic origin. Fine sands and silts occurred primarily at the western end of the northeastern corner of the grid, whereas sands mixed with pebbles and cobbles were mainly confined to the southeastern portion of the grid. Rock was encountered at several locations in this area, showing only obvious differences in substrate types.

The groups presented in the Appendix tables were derived from cluster analyses and correspond roughly to sediment distribution patterns of the area. There were two major groups of the derived dendrogram. One portion of the grid formed a wedge-shaped area ranging from inshore to offshore locations. The second major cluster consisted of stations on either side of the central group, as well as a scattering of sites at the seaward edge of that region. Both the central and peripheral areas were subdivided into several smaller groups.

Although station groups were readily delimited, a considerable number of species were about equally abundant at most stations in both of the main clusters. This species included the following: the mollusk *Parvilucina tenuisculpta*; the crustaceans *Byblis veleronis*, *Ampelisca pugetica*, *Aoroiides columbiae* and *Urothoe varvarini*; and the polychaetes *Drilonereis falcata*, *Prionospio*, near *malmgreni*, *Lumbrineris* spp. and *Terebellides stroemii*.

The ostracod *Euphilomedes carcharodonta* and the amphipod *Pardisyopia synopiae* were more abundant in the central than in the peripheral area, though they were present in both. The following species were abundant in the central region and almost completely absent from the peripheral area: The echinoderms *Amphipholis pugentana* and *Amphipholis squamata*; and the crustaceans *Clythrocerus planua* and *Idarcturus allelomorphus*.

An abbreviated list of the principal species from all groups (except Group C) is presented in Tables III.B-20 and III.B-21. A list of the principal species from eight stations sampled on the northern side of the northern channel islands is shown in Table III.B-22. It is recognized that the station grid covered only the northern island shelves and that there is no data from southern islands shelves with the exception of that of Santa Catalina Island which was so far removed from the island that it might not have been representative.

From the large number of species having over a 50 percent frequency, even over a 75 percent frequency shown in Tables III.B-4, III.B-18, III.B-19, III.B-20 and III.B-21 we might assume these species do characterize the areas or at least are widely distributed within them. An abbreviated list of the principal species from all these areas is shown in Table III.B-23.

Many of the species on this list are also important on the mainland shelf, particularly the polychaete *Lumbrineris* sp. and the bivalve

Table III.B-20

MOST FREQUENT BENTHIC INVERTEBRATES OF THE SANTA ROSA ISLAND HDSA CENTRAL REGION
From the cluster analysis groups A, B, D, and E
(Ƶ $\bar{x}$ ranged from 50 m to 108 m)

	Abundance	Frequency	
	Mean Rank	Value	Percent
Euphilomedes carcharodonta C-ostracod	3.7	31/36	86.1
Amphipholis squamata E-brittle star	3.2	30/36	83.3
Photis lacia C-amphipod	4.5	22/36	61.1
Photis californica C-amphipod	8.0	24/36	66.7
Amphipholis pugetana E-brittle star	8.2	28/36	77.8
Adroides columbae	9.7	29/36	80.1
Pagurus setosus C-decapod	16.7	29/36	80.1
[a]*Clythrocerus planua* *Idorctwurs allelomorphus*			

Source: (Taken from Jones and Fauchald, 1976).

[a]Fairly abundant in central region, completely absent from peripheral region.

Table III.B-21

MOST FREQUENT BENTHIC INVERTEBRATES OF THE SANTA ROSA ISLAND HDSA PERIPHERAL REGIONS
FROM CLUSTER ANALYSIS OF GROUPS F AND G
(Ƶ $\bar{x}$ were 162 m and 234 m)

Parvilucina tenuisculpta	1.5	17/24	70.8
Ampelisca macrocephala	5.5	10/24	41.7
Lumbrineris sp.	8.5	20/24	83.3
Tellina carpenteri	6.0	19/24	79.2
Chloeia pinnata	13.5	11/24	45.8

Source: (Taken from Jones and Fauchald, 1976).

Table III.B-22

DOMINANT BENTHIC INVERTEBRATES ON ISLAND SHELF
NORTH OF NORTHERN CHANNEL ISLAND GROUP
($\bar{z}$ = 39 m to 148 m; $\bar{x}$ = 92 m)[a]

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Lumbrineris sp. Polychaete	1	7.5	1	8/8	100.0
Pagurus setosus C-decapod crab	2	5.5	-	3/8	37.5
Aoroides columbiae C-amphipod	3	4.4	-	5/8	62.5
Photis californica C-amphipod	4	3.7	-	3/8	37.5
Euphilomedes carcharondonta C-ostracod	4	3.7	-	4/8	50.0
Micranellum crebricinctum M-snail	4	3.7	-	1/8	12.5
Sthenelanella uniformis Polychaete	-	1.7	2	6/8	75.0
Pardisynopia synopiae C-cumacean	-	2.7	2	6/8	75.0
Byblis veleronis C-amphipod	-	2.9	2	6/8	75.0
Parvilucina tenuisculpta M-bivalve	-	2.5	5	5/8	62.5
Tellina carpenteri M-bivalve	-	2.6	5	5/8	62.5
Amphiodia urtica E-brittle star	-	2.6	5	5/8	62.5
[b]*Zeuxo* sp. C-	-	(218.9)	-	(2/8)	(25.0)
Photis spp. C-Amphipod	-	(48.8)	-	(5/5)	(62.5)
Caprellidea unidentified C-amphipod	-	(6.7)	-	(2/8)	(25.0)
Cirratulidae unidentifiable Polychaete	-	(6.8)	-	(5/8)	(62.5)
Glycera sp. Polychaete	-	(1.8)	-	(6/8)	(75.0)
[b]*Amphiuridae* unidentifiable E-brittle star	-	(3.9)	-	(7/8)	(87.5)

Source: SAI (1976).

[a]Number of stations less than 100 m = 5.
Number of stations between 100 m and 250 m = 3.

[b]Possible polyspecific species with a high ranking.

Table III. B-23

FREQUENTLY OCCURRING BENTHIC INVERTEBRATES
OF NORTHERN ISLAND SHELVES

	Frequency	
	Ratio	Percent
Lumbrineris sp. polychaete	61/92	66.3
Aoroides columbiae amphipod	59/92	64.1
Parvilucina tenuisculpta bivalve	54/92	58.7
Euphilomedes carcharodonta ostracod	48/92	52.2
Tellina carpenteri bivalve	42/92	45.6

Source: Jones and Fauchald (1977) and SAI (1976).

Parvilucina tenuisculpta (Table III.B-23). The only important species, in terms of frequency on the island shelves and not also important on the mainland shelves, is the amphipod *Aoroides columbiae*.

One noticeable difference between the northern island shelves and the mainland shelves is the greater number of microcrustaceans on island shelves. This was particularly evident at the eight stations to the north of the Channel Islands where the relative dominance of crustaceans was over 67 percent compared to approximately 20 to 30 percent on the mainland shelves.

Each shelf appeared to have a somewhat distinctive group of crustaceans, although many species were the same. The only exception was Groups F and G at Santa Rosa Island which were in deeper water. A summary of these crustaceans is given below:

Santa Rosa Island

Photis spp. - Faunal groups A, B, D,
Euphilomedes carcharondonta - Faunal groups B, D, E,
Adroides columbiae Faunal group D.

San Miguel Island

Euphilomedes producta
Byblis veleronis
Heterophoxus oculatus
Paraphoxus bicuspitatus
Ampelisca pacifica

North of Northern Channel Islands

Pagurus setosus
Aoroides columbiae
Photis californica
Euphilomedes carcharondinta
Zeuxo sp.
Photis spp.

As indicated on Tables III.B-11, III.B-18, and III.B-19 from the San Miguel shelf, the relative importance of a particular crustacean species changes with depth.

With only two island shelves for comparison, conclusion may be premature, but the data presented in Table III.B-24 together with the results of Mattox (1955) indicate the biomass of the island shelves to be less than that of the mainland shelves. Data on the number of species and specimens indicate there may be no significant difference between the island and mainland shelves.

Table III.B-24

NUMBER OF SPECIES, SPECIMENS AND WET WEIGHT STANDING CROP OF HIGH DENSITY SAMPLING AREAS IN THE CALIFORNIA BIGHT

Statistical summary for the faunal associations dervied by direct inspection of the data from the Huntington Beach-Laguna Beach HDSA's.

Faunal Association	# Species		# Specimens		Mean Standing Crop (g/m^2 of Area
	Range	X	Range	X	
Shallow-Water Shelf Fauna (1)	36-65	49	108-360	263	151.9
Transitional, or Slope Fauna (2)	21-27	24	39-67	50	
Deep-Water Fauna (3)					
3A	9-12	11	21-55	38	
3B	8-14	11	13-24	20	
A & B	8-14	11	13-55	29	
Point Dume HDSA					
Shallow-Water Fauna (1)	54-70	66	120-331	236	118.3
Intermediate Fauna (2)	14-18	16	17-36	27	
Deep-Water Fauna (3)	5-12	8	5-34	17	
Coal Oil Point HDSA					
Shallow-Water, Inshore Fauna (1)	38-75	51	117-261	167	226.4
Deep-Water, Offshore Fauna (2)	4-24	13	11-32	20	
Santa Catalina Island HDSA					
Depth Range					
225-481 meters	19-38	28	31-146	65	72.0
532-851 meters	13-18	15	14-21	18	

Table III.B-24 (Cont.)

Santa Rosa Ridge - Santa Cruz Basin HDSA

	# Species		# Specimens		Mean Standing Crop (g/m^2) of Area
	Range	X	Range	X	
Shallow-Water Fauna (1)	34-53	42	61-196	102	
Intermediate Fauna (2)		4		5	38.1
Slope Fauna (3)	12-14	13	23-25	24	
Basin Fauna (4)	10-18	14	32-152	70	
San Miguel Island HDSA					
Shallow-Water Fauna (1)	58-79	69	124-202	171	104.8
Intermediate Fauna (2)	51-74	61	108-188	159	
Deep-Water Fauna (3)	20-76	37	47-230	123	
Santa Rosa Island HDSA					
	21-127	64	81-810	237	124.0
Cortes - Tanner Banks HDSA					
Bank Tops (1)	25-54	34	42-157	100	61.7
Trough Between Banks (2)	13-48	30	33-128	102	

Mainland Shelf

The early study on the benthos of the mainland shelf was a 1952 to 1954 study conducted in the San Pedro Basin and shelf (Hartman 1955, 1966). Jones (1969), summarized the papers generated from the Allan Hancock Foundation's 1956-1960 study of the mainland shelf from Point Conception to the Mexican Border. These papers include those by Barnard and Hartman (1959); Barnard, Hartman, and Jones (1959); Barnard and Ziesenhenne (1961); Given and Jones (1962); Jones (1967); and Jones and Barnard (1963). This study is also summarized by Allan Hancock Foundation (1965). Numerous accounts are available on selected groups. Some of these include: benthic amphipods (Barnard, 1963); nematodes (Jones, 1964); brachiopods (Jones and Barnard, 1963); cumaceans (Barnard and Given, 1961); ophiuroids (Barnard and Ziesenhenne, 1961). In addition, there are a number of general faunal lists associated with studies of certain geographical (natural or man-made) areas: Charisle (1969); Emerson (1970); Fauchald (1970); Pequegnat (1964); State Water Resources Control Board (1971); Turner, et al., (1964, 1966, 1968); Turner and Strachan (1969); Wintz and Fauchald (1970). Studies since the Allan Hancock study have been confined to more limited geographical locations and have concentrated on the affects of pollution on the benthic community.

The mainland shelf extends from shore to a depth of approximately 100 m (300 feet) and comprises 6.2 percent of the area from shore to the Patton Enscarpment (Allan Hancock Foundation, 1965).

This is the only benthic area of the EIS which has received extensive coverage in another study (Allan Hancock Foundation, 1965, commonly called the State Study) as well as the BLM Study. Nonetheless, the results are somewhat difficult to compare. The sampling gear was different, (orange peel grab or Van Veen grab during the State Study and a box core during the BLM Study) leading to slightly different types of sediment samples. There were relatively more samples taken closer to shore during the State Study. The mesh size of the screens used to screen the samples were similarly different (017 mm during the State Study and 1.0 mm during the BLM Study). This makes comparison of the number of individuals completely unrealistic and number of species relatively unrealistic also. One parameter which might be compared, although the difference in sampling gear and station location with respect to nearness to shore make even these comparisons tenuous, is standing crop wet weight biomass. Reish (1959) reported that 90 percent of the biomass of samples collected from Los Angeles-Long Beach Harbor was retained by a screen having a mesh opening of 1.4 mm.

The mainland shelf extends from shore to a depth of approximately 100 m (300 feet) Allan Hancock Foundation, (1965). The average standing crop biomass of the benthic macrofauna was 356 grams per sq. meter, but was reduced to about 250 g/m^2 with the exclusion of the samples dominated by the worm *Listriolobus pelodes* off Santa Barbara. Emery (1960)

reported a variation in the standing crop of the mainland shelf to be 40-4,000 grams per sq. meter. Jones and Fauchald (1976) (Table III.B-24) reported the range of the averages on the three mainland shelf areas to be from 146 g/m^2 to 214 g/m^2, slightly less than that reported by the "State Study." With the differences in sampling methods, locations and screen size, it is dangerous to conclude that there was an actual decrease in biomass since the "State Study" particularly since the difference is not extreme.

In detailed examination of 176 samples collected in the 1956-60 Allan Hancock Foundation survey, 1,473 different benthic invertebrates were identified, 63.5 percent to genus, and 11.6 percent only to higher taxonomic categories. Polychaetes (segmented annelid worms) were the most widely distributed group, outranking any other group in species, numbers, and total weight. Nearly half (355) of all specimens counted were polychaetes; 532 species were identified, and the average concentration was 1,424 organisms per sq. meter. Crustaceans, especially phoxocephalid amphipods, accounted for about 25 percent of all specimens but because of their small size, seldom comprised more than 5 percent of the biomass. They were the second largest group, with 419 species and a mean concentration of 1,352 per sq. meter. Echinoderms (brittle stars, for example) form a major group on the shelf in depths greater than 10 m. Within this group, 64 species, with an average concentration of 523 organisms per sq. meter, were identified. The small red brittle star *Amphioda urtica* was the most abundant single species, being found in 85 percent of all samples at depths greater than 10 m (30 feet), averaging 400 individuals per sq. meter. Molluscs (clams and snails) constituted the fourth group in order of abundance with 408 species and an average concentration of 368 organisms per sq. meter. Bivalve molluscs were usually so small that they contributed only a small amount to the biomass, even though they were weighed with their shells. The Echiuroid worm *Listriolobus pelodes* was not widespread, but heavily concentrated in the fine sediment area near Santa Barbara. The Branchiopod *Glotlidia albida* was found in 60 percent of the samples. The above groups accounted for over 90 percent of the benthic biomass, and the majority of the over 1,400 species that were collected.

Jones and Fauchald did not report biomass of the various taxonomic groups by depth assemblage (Table III.B-24) so are not directly comparable. However, they did report that unlike the State Study, echinoderms had the largest percentage of biomass at all three areas, ranging from nearly 40 to 50 percent.

Near Santa Barbara (Allan Hancock Foundation, 1965) reported the vast majority of specimens both in numbers and biomass (80 percent) consisted of the echiuroid worm *Listriolobus pelodes*. This species remained dominant in 1969, (Fauchald, 1971) but was greatly reduced as compared to the early 1960's at the time of the Allan Hancock

Foundation Study. This is evident in Figure III.B-5 (State Survey) and Figure III.B-6 (Pollution Study).

As far as has been determined, a study on the abundance and distribution of *L. pelodes* near Santa Barbara has not been conducted since Fauchald's Study. However, as part of his Master's thesis on their reproduction, John Pilger (personal communication) collected *L. pelodes* from the Santa Barbara area until about 1974 and indicated their population had stabilized at about 800 g/m^2, or approximately what Fauchald reported. This is a significant decrease from the State Study when concentrations as high as 2,000 g/m^2 were reached.

The Los Angeles County Sanitation District (1976) reported a large increase in the population of *L. pelodes* off Palos Verdes near the Whites Point sewage outfall. They first became abundant at areas of an intermediate distance of several miles from the outfall, then after a couple of years reached greatest abundance nearer the outfall.

Listriolobus constructs a weak U-shaped tube and is a detridal feeder, taking organic matter from the surface of the sediment. *Listriolobus* has an annual reproductive cycle with spawning peaking during a 2 to 3 month period during the spring. Fertilization is apparently external followed by the development of a trochophore larvae (the same form found in annelids and many molluscs) although neither the age at sexual maturity, nor the length of planktonic existence before settling down is known. Longevity is 3 to 4 years.

The reason for the buildup of large populations in an area is not fully understood. Allan Hancock Foundation (1965) attributed the large populations to extremely fine sediment, but recent finds by the L. A. Sanitation District indicate that fine sediment and high organic matter, provided the level of toxicants are below a certain level, may be instrumental in some population buildups.

Hartman (1955a, 1966), in her study of the San Pedro Shelf, was impressed by the patchy distribution of the benthic fauna of the California Bight. Indeed, "patchiness" has become an integral part of her interpretation of the character of the fauna of the mainland shelf of Southern California. It is her conclusion that "specific diversity in Southern California is so characteristic that large-scale communities of organisms cannot be identified" (Hartman, 1966, p.90). She makes exception only for the *Listriolobus* association of the Santa Barbara Shelf.

In spite of the difficulty, a determination of associations (termed "communities") on the mainland shelf was made by Dr. J. Laurens Barnard of the Allan Hancock Foundation Survey Staff.

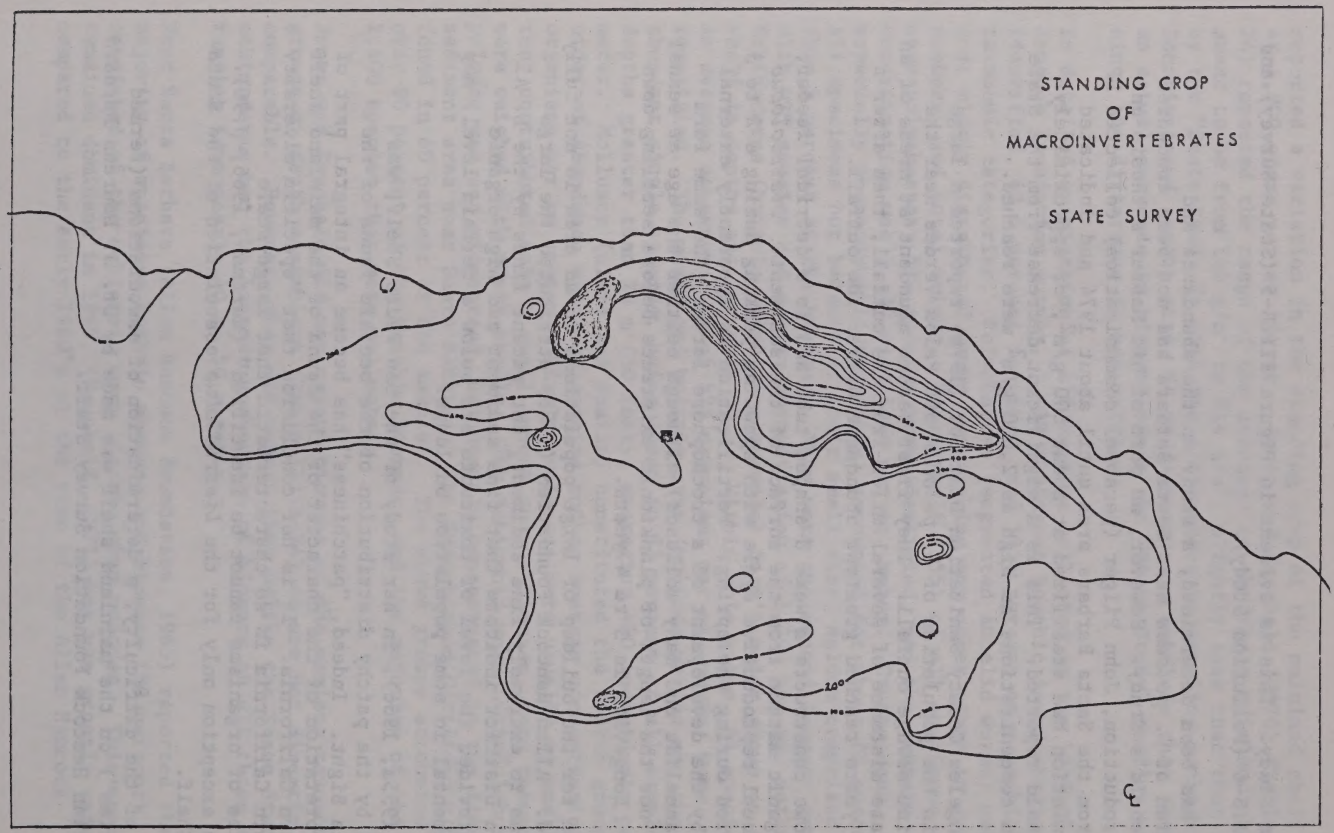


Figure III.B-5
Fauchald (1971)

Distribution of the standing crop of macro-invertebrates off Santa Barbara during the State Survey. The isopleths are in 100 grams per square meter intervals.

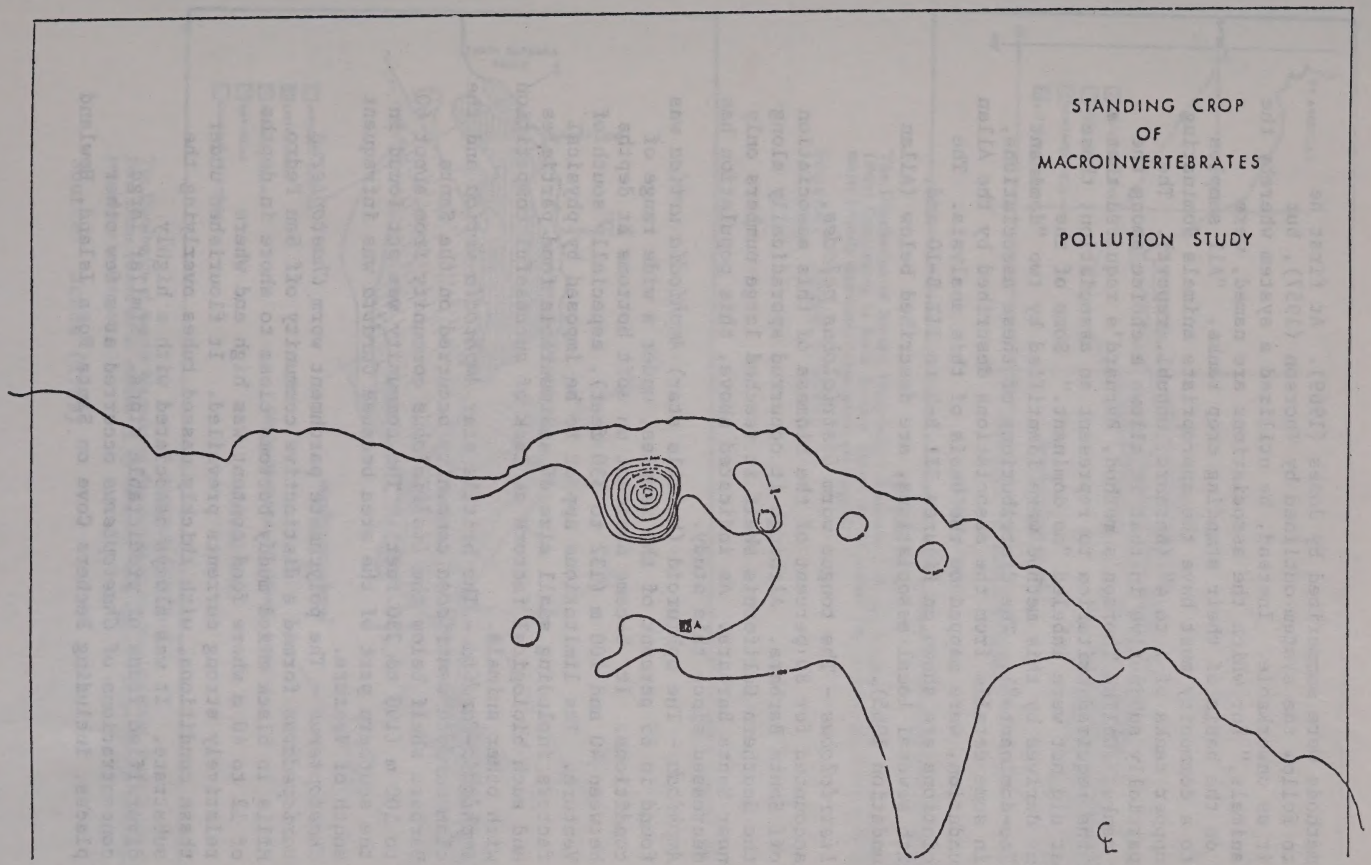


Figure III.B-6

Fauchald (1971)

Distribution of the standing crop of macro-invertebrates off Santa Barbara during the Pollution Study. The isopleths are in 100 grams per square meter intervals.

Barnard's methods were summarized by Jones (1969). At first he attempted to follow the system outlined by Thorson (1957), but abandoned it as unworkable. Instead, he utilized a system whereby the "dominant animals," for which the associations are named, were determined on the basis of their standing crop ranks. "All samples allocated to a community must have the appropriate animals dominating it in the uppper ranks of 1 to 4" (Barnard, unpubl. report). The system is partially subjective in that it allows a choice among the first four ranks. Unlike Thorson's method, Barnard's required that a sample fit the required criterion to represent an association; those samples that did not were labeled "no dominant." Some of the associations derived by this method were identified by two "dominant animals" ("co-dominants"). The distributions of these associations, differing in some details from the associations described by the Allan Hancock Foundation, were mapped on the basis of this analysis. The major associations are shown on Figures III.B-5 to III.B-10 and, together with several local associations, are described below (Allan Hancock Foundation 1965).

(1) *Listriolobus* - The tongue worm *Listriolobus pelodes*, accounted for 80 percent of the biomass of this association off Santa Barbara. Although it occurred sporadically along the Southern California shelf it reached large numbers only near Santa Barbara. As indicated above, this population has decreased since this study.

(2) *Amphioda* - The ophiuroid (brittle star) *Amphiodia urtica* was found in 85 percent of the samples, under a wide range of conditions. It became dominant on soft bottoms at depths between 40 and 100 m (132 to 330 feet), especially south of Ventura. Its limitations appear to be imposed by physical factors including small size of sedimentable food particles and such biological factors as lack of successful competition with other animals.

(3) *Amphiodia-Cardita* - The brittle star *Amphiodia urtica* and the clam *Cardita ventricosa* community occurred on the Santa Barbara shelf below the *Listriolobus* community from about 60 to 100 m (198 to 330 feet). The community was not found in the southern part of the area because *Cardita* was infrequent south of Ventura.

(4) *Chaetopterus* - The polychaete parchment worm *Chaetopterus variopedatus* formed a distinctive community off San Pedro Hills in black mixed muddy bottoms close to shore in depths of 12 to 40 m where food content was high and where relatively strong currents prevailed. It flourished under these conditions, with thickly massed tubes overlying the substrate. It was always associated with a highly diversified fauna of predictable kinds. Similar large concentrations of *Chaetopterus* occurred at a few other places, including Bechers Cove on Santa Rosa Island, Howland

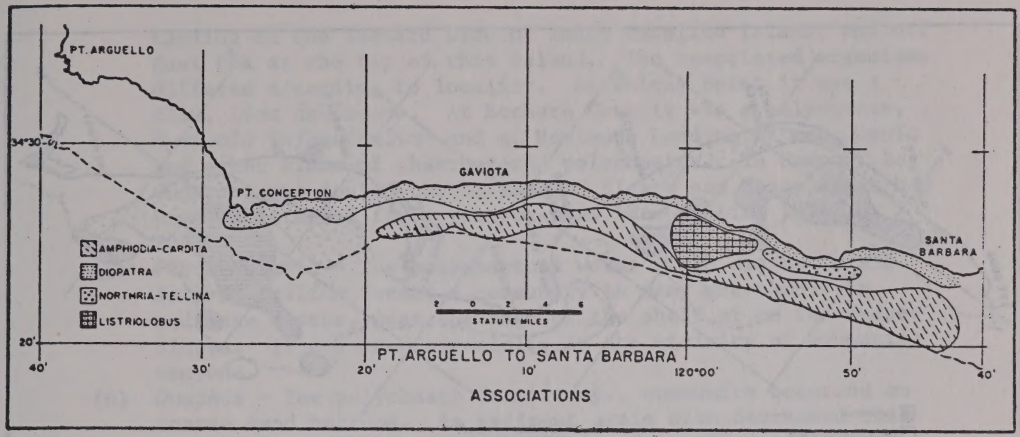


FIGURE III.B-7

The Distribution of Benthic Macrofaunal Associations on the Mainland Shelf, Point Arguello (Point Conception) to Santa Barbara (Based on an unpubl. fig. by Barnard). Note: Only the major (widely distributed) associations are mapped.

Source: Jones (1969).

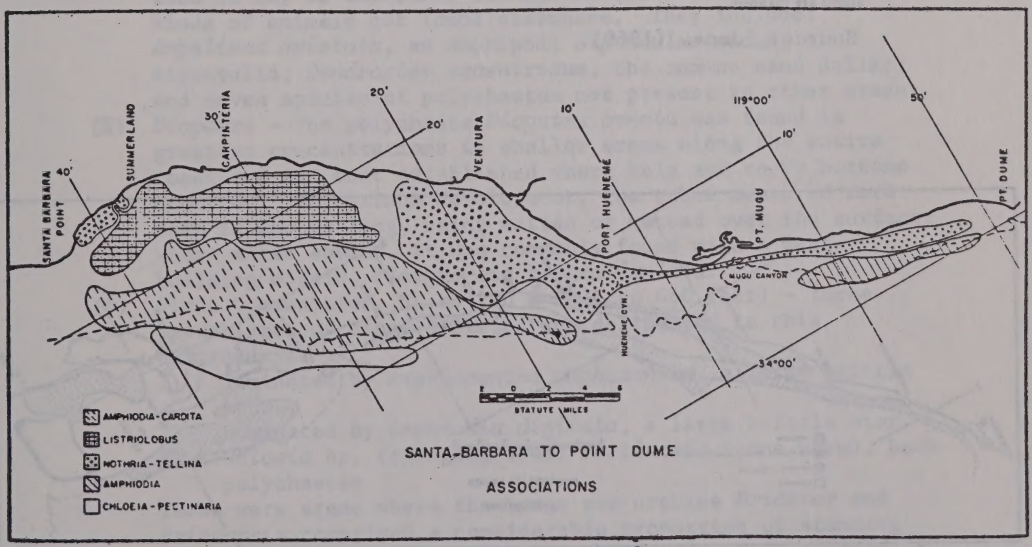


FIGURE III.B-8

The Distribution of Benthic Macrofaunal Associations on the Mainland Shelf, Santa Barbara to Point Dume (Based on an unpubl. fig. by Barnard). Note: Only the major (widely distributed) associations are mapped.

Source: Jones (1969).

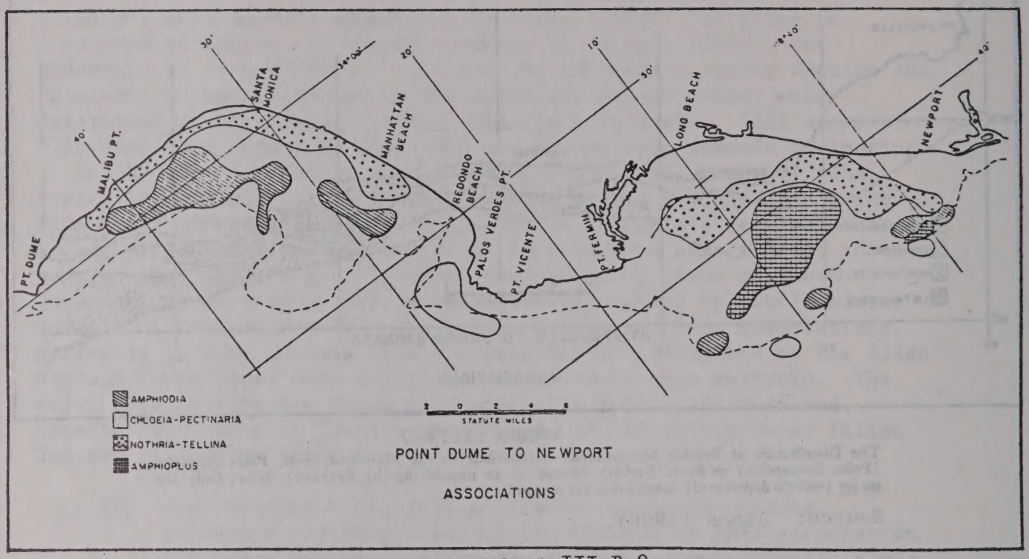


FIGURE III.B-9

The Distribution of Benthic Macrofaunal Associations on the Mainland Shelf, Point Dume to Newport (Based on an unpubl. fig. by Barnard). Note: Only the major (widely distributed) associations are mapped.

Source: Jones (1969).

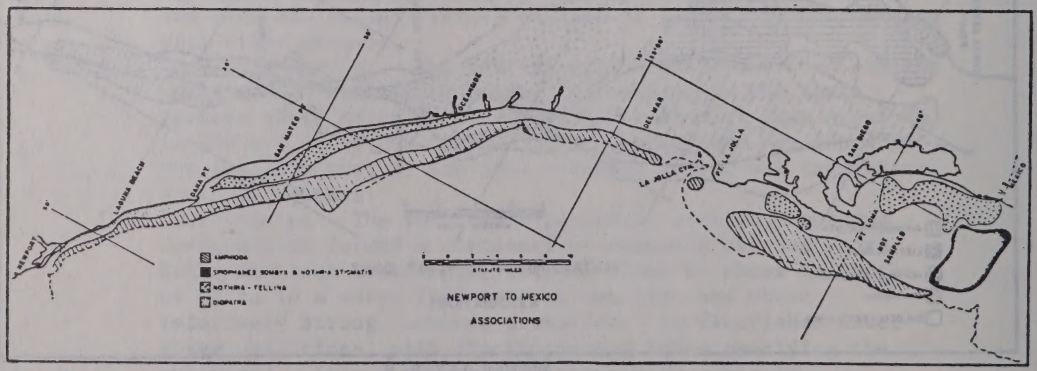


FIGURE III.B-10

The Distribution of Benthic Macrofaunal Associations on the Mainland Shelf, Newport to Mexico (Based on an unpubl. fig. by Barnard). Note: Only the major (widely distributed) associations are mapped.

Source: Jones (1969).

Landing on the leeward side of Santa Catalina Island, and off East End at the tip of this island. The associated organisms differed according to locality. At Whites Point it was a clam, *Lima dehiscens*. At Bechers Cove it was a polychaete, *Myxicola infundibulimm* and at Howlands Landing it was *Owenia* and other kinds of chaetopterid polychaetes. In Newport Bay *Chaetopterus* fouled the bottoms of floats and boats which had been undisturbed for a year or more (MacGinitie, 1938, p. 209).

(5) *Pista-Nothria* - The polychaetous worms *Pista disjuncta* and *Nothria pallida* formed a community in many green muds in moderate depths, near the edge of the shelf or on the deeper slopes. It occurred especially in the vicinity of submarine canyons.

(6) *Onuphis* - The polychaete *Onuphis* sp., community occurred on coarse sand bottoms. As sediment grain size decreased this community graded into and was replaced by the *Amphiodia urtica* community.

(7) *Blepharipoda-Branchiostoma* - The spiny sand crab *Blepharipoda occidentalis* and the cephalochordate *Branchiostoma californiensis* (known to biology students as amphioxus) formed a sharply limited community where red and brown sands occurred. The associated organisms were more sharply limited than in any of the other communities, since they were often kinds of animals not found elsewhere. They include: *Ampelisca cristata*, an amphipod; *Sipunculus nudus*, a sipunculid; *Dendraster excentricus*, the common sand dollar; and seven species of polychaetes not present in other areas.

(8) *Diopatra* - The polychaeta *Diopatra ornata* was found in greatest concentrations in shallow areas along the entire coast and was best established where kelp and rocky bottoms occurred. At maximum development, the tubes measured more than 12 inches long, being matted or massed over the surface. Where algae abound, it was commonly found with a nest-building nereid, *Platynereis bicanaliculata*.

(9) Slope Communities, 67 to 200 m (221 to 660 feet) - Three assemblages of broad distribution delineated in this environment.

1) Dominated by *Amphiacantha amphacantha*, a large brittle star.
2) Dominated by *Amphiodia digitata*, a large brittle star.
3) *Chloeia* sp, (stinging worm) *Pectinaria* (cone worm), both polychaetes.

These were areas where the large sea urchins *Briaster* and *Brissopsis* comprised a considerable proportion of standing crop so that slope communities maintained as high a standing crop as communities in shelf waters, 10 to 67 m (3 to 221

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feet). Nevertheless, the small amount of existing organic matter in sea urchins and the probability that they grow slowly and have a low turnover are factors of importance in comparing raw data of standing crop between shelf and slope.

(10) Rocky Bottoms - Several rocky bottom communities might be identified, but rocky outcrops are relatively sparse and difficult to sample with the gear used. Most animals are epifaunal, either attached to the rocks, or existing in crevices. Representative species are a seastar, *Asterina*, a large snail, *Astraea undosa*, a surface brittle star, *Ophiothrix spiculata*, a stalked barnacle, *Scalpellum*, and other animals.

(11) Some Small Communities - Possibly the following communities are recognizable, but they were of small extent in Southern California. Most of them have been recovered in less than five samples, but they appeared to be distinct types of assemblages.

(a) *Dendraster* sp. The sand dollar community in sands in shallow water. May be mixed with *Chaetopterus*.

(b) *Ophiura lutkeni*. A deep water ophiuroid brittle star assemblage.

(c) *Ampelisca*. A deep water gravel community dominated by this tube-building amphipod.

(d) *Pherusa-Onuphis*. A dominant complex recovered in three samples around the Whites Point outfall to a near exclusion of other animal species. Both animals are polychaetes.

(e) *Capitella*. This polychaete, reported as an indicator of diluted sea-water and also of polluted areas in enclosed bays and harbors, dominated several samples. Two or three of the samples were probably indicative of natural pollution as a result of the metabolic activities of other epifaunal animals, whose fecal matter falls to the bottom and provides a rich organic mud. This is especially the condition in beds of *Diopatra* in kelp and algal fields.

(f) *Tharyx*. The tube-building worm *Tharyx tesselata* dominated a number of samples on the San Pedro Shelf just off the breakwater. It might be considered an indicator of low levels of pollution, either man-made or natural, because the animal also dominates other samples where naturally produced dark gray or black sediments occur. Reish (1959) considered *Tharyx parvus* an indicator of "healty bottom" in Los Angeles Harbor. Notwithstanding, some of the muds it occupied were black and, for open sea areas, this is most certainly indicative of an oversupply of organic matter. Species of *Tharyx* were widespread and numerous through about 15 percent of the total samples taken, and their presence

alone is not an indicator of pollution. "Perhaps the numerical frequency in relation to surrounding samples may be of some use in pinpointing degrees of pollution."

On the basis of the samples spaced statistically according to area, an estimate has been made of the areas occupied by some of the principal communities, with results as shown on Table III.B-25.

The method of classifying benthic communities based upon a dominant species, reported above, emphasizes distinctiveness at the expense of similarities. Widely distributed species were sometimes omitted from the descriptions. Small but numerically abundant forms, particularly polychaetes and amphipods, tend to be omitted from the descriptions of these associations (Jones, 1969). Jones reported that relatively few of the species collected in the Hancock Foundation shelf survey were both frequent (found in 40 percent or more of 176 samples) and resonably numerous (15 or more specimens/sq. m). Table III.B-26 lists the 24 species that might be designated "prevalent," in terms of their frequency of occurrence and population density. These 24 species (and the four other groups listed in the table) comprised only 1.6 percent of the total macroinvertebrate species found on the mainland shelf. Nevertheless, because they are nearly ubiquitous, relatively abundant, and found frequently with a number of other species, these organisms may be considered the major faunal elements on the mainland shelf.

The diagramatic representation of the inhabitants of a typical one-quarter square meter of bottom soil in the *Listriolobus* association presented by Barnard and Hartman (1959) did not include six species which these authors considered prominent members of this association. These are *Ceratocephala c. americana* (means density 76/m^2), *Marphysa* sp. (40/m^2), *Hesperonoe* sp. (56/m^2), *Sternaspis fossor* (16/m^2, *Amphiodia urtica* (98/m^2) and *Saxicavella pacifica* (93/m^2). Together they represent a population of 370 specimens per square meter. The omission of *Amphiodia urtica* is particularly noteworthy. The mean density of *Amphiodia urtica*, (98/m^2), is nearly a fourth of that in the *Amphiodia-Cardita* association (408/m^2) and almost one-half that in the *Amphioplus hexacanthus* association. The presence of important species such as this should not be obscured in the process of faunal description.

It is noteworthy that of the seven most frequently occurring species collected from the mainland shelf during the BLM Study (Table III.B-27) four, (assuming *(Lumbrineris* sp. = *L. cruzensis*) were also listed by Jones in Table III.B-26 as species typical of the mainland shelf. The ostracod *Euphilomedes* was probably omitted only because of the inability to identify this group during the State Study. This leaves only the bivalve *Parvilucina tenuisculpta* and other molluscs listed as

Table III.B-25

DOMINANCE OF BENTHIC COMMUNITIES ON THE SOUTHERN CALIFORNIA MAINLAND SHELF, SPACED STATISTICALLY ACCORDING TO AREA, BASED ON 150 STATIONS

	Percent of Total shelf area
Amphiodia	23
Listriolobus	7
Onuphis	6
Amphiodia/Pectinaria	5
Nothria spp.	5
Amphiodia/Cardita	4
Diopatra	4
Cardita	3
Astropecien	1
Chloeia	1
Chactopterus/Lima	1
Sternaspis	1
Amphiodia/Onuphis	1
Lytechinus	1
Tharys	1
	67
Diversified and unclassified	33
TOTALS	100

From: Allan Hancock Foundation (1965).

Table III.B-26

COMMON BENTHIC INVERTEBRATES IN THE SOUTHERN CALIFORNIA MAINLAND SHELF[a]

	Frequency of Occurrence (percent)	Density (no./sq m)	Density Rank
POLYCHAETES			
Prionospio pinnata	90.4	28.0	
Prionospio malmgreni	84.5	92.8	2
Pectinaria californiensis	74.5	45.3	9
Pholoe glabra	71.1	51.1	5
Paraonis gracilis	61.3	48.3	6
Spionphanes missionensis	60.8	22.8	
Tharyx tesselata	59.7	53.6	4
Haploscoloplos elongatus	59.7	31.7	
Sternaspis fossor	54.0	15.7	
Glycera capitata	53.3	17.6	
Lumbrineris cruzensis	52.3	35.9	
Cossura candida	51.7	45.8	8
Nephtys sp.	51.2	24.2	
Aricidea lopezi	45.5	28.7	
CRUSTACEANS			
Ostracods unknown	61.9	279.9	b
Tanaids unknown	59.7	26.3	
Ampelisca brevisimulata	57.4	35.7	
Heterophoxus oculatus	55.0	23.8	
Ampelisca cristata	50.5	22.9	
Paraphoxus bicuspidatus	43.8	47.6	7
Paraphoxus similis	43.2	17.4	
Metaphoxus frequens	41.5	18.0	
ECHINODERMS			
Amphiodia urtica	87.0	359.1	1
Amphipholis squamata	77.3	39.5	10
MOLLUSCS			
Axinopsida serricata	52.3	54.7	3
OTHER TAXA			
Nemerteans unknown	100.0	28.0	
Nematodes unknown	51.7	27.2	
Glottidia albida	51.7	24.2	

[a]From Jones (1967, 1969).
[b]Not ranked (comprises several species).

Table III. B-27
MOST FREQUENTLY OCCURRING BENTHIC INVERTEBRATES OF MAINLAND SHELF AND SLOPE

	Abundance	Frequency	
	Mean of the Means	Ratio	Percent
Lumbrineris sp. Polychaeta	3.8	79/98	80.6
Parvilucina tenuisculpta bivalve	7.0	69/98	70.4
Axinopsida serricata bivalve	5.6	67/98	68.4
Amphiodia urtica brittle star	10.0	59/98	60.2
Heterophoxus oculatus amphipod	2.4	52/98	53.1
Pectinaria californiensis Polychaete	2.1	51/98	52.0
Euphilomedes carcharodonta Ostracod	5.7	49/98	50.0

Other common species

Tellina carpenteri bivalve
Mysella tumida bivalve
Prionospio near *malmgreni* polychaete
Euphilomedes producta ostracod
Paramya sp. bivalve

Frequent benthic invertebrates on the slope:

Pectinaria californiensis polychaete
Limifossor fratula shelless aplocophoran
Ampelisca macrocephala amphipod
Cyclocardia ventricossa bivalve

Source: Jones and Fauchald (1977) and SAI (1977).

other common species on Table III.B-27 missing from the Stat's Survey list.

This document is a fair agreement between the most common species reported from the two studies on the mainland shelf. This was also supported by Jones (personal communication) who has examined the raw data of each study from certain mainland shelf HDSA's.

With the exception of the shelf off Palos Verdes, there was essentially a continuous areal coverage of the mainland shelf from Point Mugu Lagoon to Dana Point during the BLM benthic baseline study conducted 1975-1976. In addition to this, there was an area sampled off Coal Oil Point. Although the mainland shelf adjacent to the Santa Barbara Channel and the shelf between Dana Point and San Diego were not sampled during the first year's effort, several transects, of far lesser areal extent at Point Conception, Goleta Point, Oceanside, and San Diego are being sampled during the second year effort. This will significantly extend the areal coverage to include at least a glimpse of the entire mainland shelf off Southern California.

Not all of the coverage between Point Mugu and Dana Point was high density sampling areas; the breakdown of the difference is given below;

HDSA	Non-HDSA
Coal Oil Point	Point Mugu to Point Dume HDSA
Point Dume	Santa Monica Bay
Huntington-Laguna Beach	San Pedro Shelf

The most numerous and frequent species of each assemblage and depth are listed in Tables III.B-28 through III.B-34, and the most common species in terms of frequency from all areas are listed in Table III.B-27.

The two assemblages at Coal Oil Point (Tables III.B-28 and III.B-29) were combined because they are both relatively shallow and still have a greater than 70 percent frequency of occurrence. With the relatively high number of species this frequent, it appears that these species are indicative of the area which is relatively well defined in terms of depth homogenity. The species common at this area which are not nearly as common at the other mainland shelf areas are:

amphipod	*Byblis veleronis*
cumacean	*Eudorella pacifica*
amphipod	*Listriella goleta*
polychaete	*Maldane sarsi*

Of these species, *Byblis veleronis*, and *Eudorella pacifica* may be somewhat distinctive of this area. As with the northern island shelf, microcrustaceans appear to reach higher abundance and are represented by more species than those areas to the south.

The few species having a high frequency of occurrence (only *Glycera* sp. greater than 70 percent) at stations between Point Mugu and Point Dume HDSA indicates it may be a diverse area without representative dominant species and/or there may be too great a depth range to document a homogenous area in terms of the frequency dominant species (Table III.B-30). For example, the amphipod *Amphlisco macrocephala*, which was present at 53 percent of the stations, appears to be more characteristic of the slope areas. Species common of this area, particularly in comparison to the other mainland shelf areas, and may be somewhat distinctive of it, are:

the echiuroid worm	*Listriolbus pelodes*
the sipunculid worm	*Golfingia improvisa*
amphipods	*Ampelisca catalinensis* and *Ampelisca macrocephala*

Some of these species, particularly *A. marcrocephala*, may be more characteristic of the slope areas than the shelf.

The Point Dume shelf HSDA (Table III.B-31), with 10 species collected at over 75 percent of the stations, appears to be fairly uniform in terms of depth and the frequent species representative of the area. Only the amphipod *Ampelisca pacifica*, with 62.5 percent frequency, was collected in greater frequency here than at the other mainland shelf areas and may be somewhat distinctive of this area.

The Santa Monica Bay area (Table III.B-32) with only three species having greater than 70 percent frequency of occurrence, may be a diverse area without representative dominant species and/or there may be too great a depth range to document a homogeneous area even in terms of the frequency dominant species. The mollusc *Acila castrensis* and polychaetes of the genus *Mijriochele* occur here in greater numbers than at other mainland shelf areas and may be disinctive of the area. Low

Table III.B-28

DOMINANT BENTHIC INVERTEBRATES OF THE SHALLOW-WATER INSHORE ZONE (Z<100 m) ASSEMBLAGE AT COAL OIL POINT HDSA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
[a]*Amphiodia urtica* brittle star	1	10.5	2	9/11	81.8
Crustacea					
Euphilomedes carcharondonta ostracod	2	7.7	4	8/11	72.7
Euphilomedes producta ostrocod	5	5.2	15	5/11	45.4
[c]*Paraphoxus bicuspidatus* amphipod	12	1.8	23	4/11	36.4
Listriella goleta amphipod	26	0.8	20	4/11	36.4
Mollusca					
Parvilucina tenuisculpta bivalve	4	5.7	6	8/11	72.7
Mysella tumida bivalve	6	3.6	5	8/11	72.7
Axinopsida serricata bivalve	9	2.0	3	8/11	72.7
[b]*Nuculana taphria* bivalve	28	0.7	32	3/11	27.3
[b]*Paramya* sp. bivalve	15	1.4	22	4/11	36.4
[c]*Tellina carpenteri* bivalve	24	0.9	17	5/11	45.4
[b]*Macoma yoldiformis* bivalve	21	1.0	-	2/11	18.2
Polychaeta					
Lumbrineris sp.	3	6.0	1	11/11	100.0
[c]*Mediomastus californiensis*	11	1.9	21	4/11	36.4
Minor Phyla					
Echiurida- *Listriolobus pelodes*	17	1.1	13	6/11	54.5

Source: Jones and Fauchald 1976.
[a]The characteristic species of the zone.
[b]Common by visual inspection.
[c]Very abundant at shallowest inspection.

Table III.B-29

DOMINANT BENTHIC INVERTEBRATES OF THE DEEPER SHALLOW-WATER INSHORE ZONE (Z>100 m) ASSEMBLAGE AT COAL OIL POINT HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
[a]*Amphiodia urtica*	1	12.0	3	6/8	75.0
Crustacea					
Euphilomedes producta ostracod	2	6.7	10	4/8	50.0
Euphilomedes carcharondonta	5	2.9	9	4/8	50.0
[a]*Byblis veleronis* amphipod	19	1.0	2	7/8	87.5
Eudorella pacifica cumacean	14	1.6	5	6/8	75.0
Heterophoxus oculatus amphipod	16	1.4	5	6/8	75.0
Mollusca					
Cyclocardia ventricosa bivalve	6	2.4	19	3/8	37.5
Axinospisda serricata bivalve	7	2.1	4	6/8	75.0
Mysella tumida bivalve	12	1.7	7	5/8	62.5
Paramya sp. bivalve	9	1.9	13	4/8	50.0
Polychaeta					
Lumbrineris sp.	3	5.5	1	8/8	100.0
Maldane sarsi	4	3.9	20	3/8	37.5
Harmothoe lunulata	17	1.2	11	4/8	50.0

Source: (Jones and Fauchald, 1977).

[a]The distinguishing characteristic species of the zone.

Table III.B-30

DOMINANT BENTHIC INVERTEBRATES OF COASTAL BOTTOMS
NORTH OF THE POINT DUME HIGH DENSITY SAMPLING AREAS TO MUGU LAGOON
(Z = 22 m to 741 m; $\bar{x}$ = 269 m)[a]

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Amphiodia urtica E-brittle	1	11.6	1	8/15	53.3
Listriolobus pelodes Echiuroid	2	11.3	-	4/15	26.7
Euphilomedes carcharondonta C-ostracod	3	4.3	-	6/15	40.0
Aoroides columbiae C-	4	3.1	-	5/15	33.3
Ampelisca catalinensis C-amphipod	5	3.0	-	3/15	20.0
Golfingia near *imprisca* sipunculid	6	2.7	-	1/15	6.7
Parvilucina tenuisculpta M-clam	-	1.8	1	8/15	53.3
Ampelisca macrocephala C-amphipod	-	2.5	1	8/15	53.3
Tellina carpenteri M-clam	-	1.9	4	7/15	46.7
Lumbrineris sp. Polychaete	-	1.6	4	7/15	46.7
Pectinaria californiensis Polychaete	-	1.0	4	7/15	46.7
[b]*Glycera* sp. Polychaete	-	(2.8)	-	(11/15)	(73.3)
Amphiodia sp. E-brittle star	-	(8.2)	-	(8/15)	(53.3)
Photis spp. C-amphipod	-	(5.7)	-	(6/15)	(40.0)

Source: (From SAI, 1976).

[a]Number of Stations less than 100 m = 5.
Number of Stations between 100 m and 250 m = 5.

[b]Possible polyspecific species with high rankings.

Table III.B-31

DOMINANT BENTHIC INVERTEBRATES OF THE SHALLOW-WATER FAUNA (Z = 40 m to 193 m; x = 93 m) ASSEMBLAGE AT POINT DUME HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
[a]*Amphiodia urtica* brittle star	2	18.5	7	6/8	75.0
Crustacea					
Euphilomedes producta ostracod	1	20.9	10	6/8	75.0
Paraphoxus bicuspidatus amphipod	4	5.7	4	7/8	87.5
Heterophoxus oculatus amphipod	8	4.5	2	7/8	87.5
Ampelisca pacifica amphipod	31	0.6	15	5/8	62.5
Mollusca					
[a]*Axinospida serricata* clam	3	9.1	1	8/8	100.0
[a]*Parvilucina tenuisculpta* clam	13	3.0	5	7/8	87.5
"Characteristic to a lesser extent"					
[b]*Mysella tumida* clam	16	2.1	22	4/8	50.0
[b]*Cylichna attonsa* snail	19	1.5	26	3/8	37.5
[b]*Tellina carpenteri* clam	20	1.5	24	4/8	50.0
[b]*Volvulella panamica* snail	22	1.4	14	6/8	75.0
Polychaeta					
Mediomastus californiensis	5	5.5	17	5/8	62.5
Prionospio malmgreni	6	5.1	6	7/8	87.5
Lumbrineris sp.	12	3.0	3	7/8	87.5
Pectinaria californiensis	7	5.0	11	6/8	75.0
Terebellides stroemi	27	1.0	13	6/8	75.0
Minor Phyla					
Listriolobus pelodes Echiuroida	24	1.2	38	2/8	25.0
[b]*Phoronis* sp. Phoronida					
[b]*Glottida albida* Branchiopoda					
[b]*Edwardsiae* sp. Cnidaria					

Source: (Jones and Fauchald, 1977).
[a]The characteristic species of the zone.
[b]Common by visual inspeciton.

Table III.B-32

PRINCIPAL BENTHIC INVERTEBRATES IN SANTA MONICA BAY
($\bar{z}$ 29 m 748 m; $\bar{x}$ = 206 m)[a]

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Parvilucina tenuisculpta M-bivalve	1	18.3	1	21/24	87.5
Axinopsida serricata M-bivalve	2	17.1	2	19/24	90.5
Amphiodia urtica E-brittle star	3	5.6	-	7/24	29.2
Acilacartrensis M-	4	4.3	-	4/24	16.7
Euphilomedes carcharondonta C-ostracod	5	3.4	-	7/24	29.2
Lumbrineris sp. Polychaete	-	1.5	3	17/24	70.8
Pectinaria californiensis Polychaete	-	3.0	4	16/24	66.7
Heterophoxus oculatus C-amphipod	-	2.9	5	15/24	62.5
Prionospio near *malmgreni* Polychaete	-	2.0	6	12/24	50.0
Eudorella pacifica C-cumacean	-	0.8	7	11/24	45.8
Tellina carpenteri M-bivalve	-	2.1	7	11/24	45.8
		(16.7)	-	(1/24)	(4.2)
[b]*Myriochele* spp. (Oweniidae) Polychaete	-	(4.5)	-	(2/24)	(8.3)
Mycoma sp. M-bivalve	-	(7.6)	-	(12/24)	(50.0)
Amphiodia sp. E-brittle star	-	(6.3)	-	(7/24)	(29.2)

Source: (From SAI, 1976).

[a]Number of Stations less than 100 m = 10.
Number of Stations between 100 m and 250 m = 5.

[b]Possible polyspecific species with high rankings.

frequencies (17 and 12 percent) and the relatively high abundances of a mean of 4.3 and 16.7 for the entire Santa Monica Bay area may indicate these species occur in large numbers, but have a restricted distribution at some area or limited depth in Santa Monica Bay.

The San Pedro Shelf area, with 5 species or species groups having a frequency of over 70 percent, and 6 other species with a 50 percent or greater frequency (Table III.B-33) appears to be a fairly homogeneous area. Those species with the highest frequencies are representative of it. The polychaete *Cirratlidae* sp. and the unidentified nematode were collected far more frequently here than at the other mainland shelf areas and may be somewhat distinctive of this area.

The Huntington-Laguna Beach HDSA (Table III.B-34) had 5 of the 8 most common species with a 70 percent or greater frequency indicating it to be a homogeneous area, particularly in terms of depth and the most frequent species. Only the amphipod *Westwoodilla caecula* (55.5 percent frequency) may be somewhat distinctive of this area.

Table III.B-27, shows there were 7 species collected in 50 percent or more of all samples taken on the mainland shelf. The fact that some of the stations were in deeper water than the 100 m (330 feet) limit of the mainland shelf makes the species present with high frequency even more significant. This was not expected from some of the previous literature which emphasized the patchiness of the benthos of the Southern California area.

When considering the assemblage in its entirety, the area is not nearly as homogeneous as the cluster analyses of Jones and Fauchald (1977) indicate; that under similar conditions of depth, sediment type, distance from the mainland coast, etc., certain species tend to be found somewhat consistently in relatively high number of individuals, particularly on the central mainland coast in terms of frequency, the polychaete *Lumbrineris* sp. was most frequently collected but the brittle star *Amphiodia utica* was significantly more numerically abundant than any other species. The 60 percent frequency of occurrence in the BLM Study was somewhat less than the 85 percent frequency in the State Study, although a wide distribution of this species occurred during both studies.

The general agreement between Jones (1969) and 24 most common species and those in Table III.B-27 has been mentioned above. Although it would be desirable to evaluate the relationship between the mean number of species, specimens or standing crop of the different areas, there does not appear to be a consistent relationship (Table III.B-24).

SCCWRP (1973) reported a relationship between the relative abundance of the bivalve *Parvilucina tenuisculpta* and the brittle star *Amphiodia urtica* near the old and the new Orange County outfalls both prior to,

Table III.B-33

DOMINANT BENTHIC INVERTEBRATES FROM SAN PEDRO SHELF
($\bar{z}$ = 17 m to 240 m; $\bar{x}$ = 52.6 m)[a]

	Abundance		Frequency		
	Rank	Value Mean No./	Rank	Value	Percent
Parvilucina tenuisculpta M-clam	1	10.7	2	11/14	78.6
Lumbrineris sp. Polychaete	2	4.8	1	12/14	85.7
Euphilomedes carcharondonta C-ostracod	3	4.8	3	9/14	64.3
Prionospio near *malmgreni* Polychaete	4	3.6	5	8/14	57.1
Tellina carpenteri M-clam	5	3.2	3	9/14	64.3
Axinopsida serricata M-clam	6	2.7	-	7/14	50.0
Pectinaria californiensis Polychaete	-	1.7	5	8/14	57.1
Macoma yoldiformis M-clam	-	1.3	5	8/14	57.1
[b]Cirratulidae, sp. Polychaete	-	(8.1)	-	(11/14)	(78.6)
[b]*Glycera* sp. Polychaete	-	(2.9)	-	(10/14)	(71.4)
[b]Amphiuridae unidentifiable E-brittle star	-	(5.8)	-	(7/14)	(50.0)
[b]Nemertea unidentified	-	(3.2)	-	(14/14)	(100.0)

Source: (From SAI, 1976).

[a]Number of stations less than 100 m = 13.

[b]Possible polyspecific species with high rankings.

Table III.B-34

DOMINANT BENTHIC INVERTEBRATES OF THE SHALLOW-WATER SHELF FAUNA (Z = 28 m to 109 m) ASSEMBLAGE AT HUNTINGTON-LAGUNA BEACH HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
[a]*Amphiodia urtica* brittle star	5	6.9	4	14/18	77.8
Crustacea					
Euphilomedes producta ostracod	1	20.7	29	5/18	27.8
Euphilomedes carcharondonta ostracod	2	14.0	9	11/18	61.1
Heterophoxus oculatus amphipod	6	5.4	3	15/18	83.3
[a]*Paraphoxus bicuspidatus* amphipod	17	1.5	16	8/18	44.4
[b]*Westwoodilla caecula* amphipod	20	1.2	12	10/18	55.5
[b]*Pinnixa schmitti* decapod crab	24	0.8	21	7/18	38.9
Mollusca					
Parvilucina tenuisculpta clam	3	9.5	5	14/18	77.8
Paramya sp. clam	4	7.2	12	9/18	50.0
Axinopsida serricata clam	7	4.9	2	15/18	83.3
Mysella tumida clam	14	2.3	6	13/18	72.2
Polychaeta					
Lumbrineris sp.	8	4.3	1	17/18	94.4
[b]*Mediomastus californiensis*	9	4.1	8	12/18	66.7
[b]*Pholoe glabra*	21	1.0	17	8/18	44.4
[b]*Pectinaria*	13	2.4	13	9/18	50.0

Source: Jones and Fauchald 1976.

[a] Jones and Fauchald 1976.
[b] Common by visual inspection.

and following the initiation of discharge through the new outfall. There was a marked increase in the ratio of brittle stars to *P. tenuisculpta* after termination of discharge. *P. tenuisculpta* was more abundant during discharge and brittle stars were more abundant after termination of discharge. At the new outfall, a year after initiation of discharge, the ratio was not very different from predischarge values, with brittle stars outnumbering *P. tenuisculpta*, the number of both organisms having increased.

At first, it appears (Table III.B-35) that Santa Monica Bay and San Pedro Shelf have fewer *A. urtica* than the other areas, and it might be desirable to speculate that this is because of the greater discharge of pollutants into these areas. This is particularly appealing, because the apparently more pollution-tolerant clam *P. tenuisculpta* reaches its greatest abundance in these same two areas. However, because of the greater depth range in these two areas, and the relatively low numerical abundance of *A. urtica* at Huntington-Laguna Beach, these conclusions may be tentative.

Table III.B-35

MEAN NUMBER PER AREA AND THE ROUNDED PERCENT FREQUENCIES OF *AMPHIODIA URTICA* AND *PARVILUCINIA TENUISCULPTA* ON THE MAINLAND SHELF

	Amphiodia urtica		*Parvilucinia tenuisculpta*	
Area	Abundance	% Frequency	Abundance	% Frequency
Coal Oil Point (Ƶ J 100 m)	12.0	75	5.7	73
Coal Oil Point (Ƶ F 100 m)	10.5	82		
Mugu to Point Dume HDSA	11.6	53	1.8	53
Point Dume	18.5	75	3.0	87
Santa Monica Bay	5.6	29	18.3	87
San Pedro Shelf	1.8	43	10.7	79
Huntington-Laguna Beach	6.9	78	9.5	78

Fay (1972) reported the shallower areas of Santa Monica Bay to have a greatly reduced fauna in comparison with surrounding areas.

Work by SCCWRP reported by Word, Myers, and Mearns (1977) also support the relationship between *P. tenuisculpta* and *Amphiodia urtica* in polluted areas (Figure III.B-11). These samples were taken at 60 meters around 5 sewage outfalls (Ventura, Hyperion, Whites Point, Orange County and Point Loma) in the California Bight.

Parvilucina reached large populations (approximately 3,500 individuals g/m^2) and accounted for over 60 percent of the individuals in the samples at the "polluted" B category while *Amphiodia* sp. (most *A. urtica*) was absent (Figure III.B-11). The areal distance of this "polluted" B category ranged from 0.5 km to 5.6 km from (0.31 to 3.5 miles) from the outfalls. The transitional areas had a gradual decrease in the number of *P. tenuisculpta* to $500/m^2$ and 30 percent of the population and an increase to $50/m^2$ of *Amphiodia urtica*.

The deep water fauna of the Huntington-Laguna Beach and Point Dume HDSA are show in Tables III.B-36 and III.B-37. There was not a lot of obvious correlation between the frequent and abundant species of the areas nor were many species present with much frequency. The gastropod *Mitrella permodesta* and bamboo worms (*Maldane* spp.) and to a far lesser extent, the bivalve *Mysella compressa* were the only species relatively common to both areas.

Jones and Fauchald (1977) divided the soft bottoms of Tanner-Cortes Banks into a bank-top assemblage and a bank-trough assemblage (Tables III.B-38 and III.B-39). *Amphidia urtica* and *Parvilucina tenuisculpta* are also relatively important here. Recent analysis by Jones (personal communication) indicates that these assemblages are significantly different from the other HDSA assemblages of the Bight. The highly productive and unusual hard bottoms of these banks are of even greater interest, however.

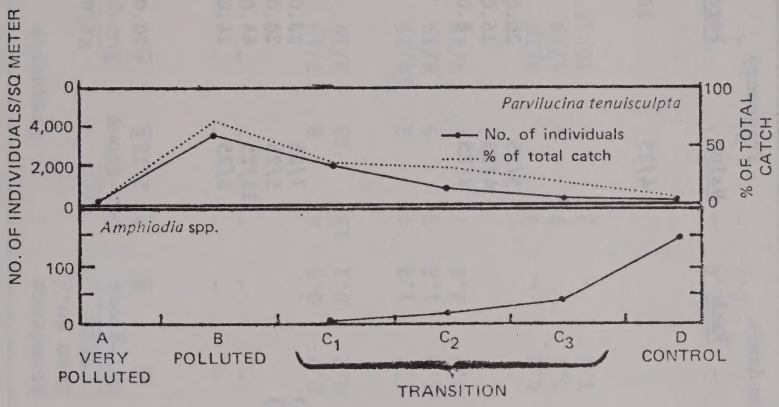


Figure III.B-11 Mean abundance of the clam *Parvilucina tenuisculpta* and brittle stars *Amphiodia* spp. at stations representing different categories of pollution.

Table III.B-36

DOMINANT BENTHIC INVERTEBRATES OF THE COMBINED SUB AREAS OF THE DEEP-WATER FAUNA (522 m to 744 m; $\bar{x}$ = 620 m) ASSEMBLAGE AT POINT DUME HIGH DENSITY SAMPLING AREA

	Abundance		Frequency	
	Rank	Rank	Value	Percent
Echinodermata				
[b]*Ophiomusium jolliensis* brittle star	12		4/25	16.0
[b]*Ophioscolex* sp. brittle star				
[b]*Asteronyx loveni* brittle star				
[b]*Myxoderma platyacantha* star fish				
Crustacea				
Ampelisca macrocephala amphipod	4		5/25	20.0
Heterophoxus oculatus amphipod	5		4/25	16.0
Ampelisca catalinensis amphipod	16		2/25	8.0
Biblis tannerensis amphipod				
Harpiniopsis spp. amphipod				
Leucon sp. cumacea				
Diastylis cumacea				
Mollusca				
[a]*Mitrella permodesta* snail	1(A)		7/25	28.0
[a]*Mysella compressa* bivalve	1(B)		5/25	20.0
Tomburchus redondoensis bivalve	2		11/25	44.0
Limifossor fratula aplochophora	10		6/25	24.0
[b]*Chaeotderma* spp. aplachophora				
Polychaeta				
Maldane glebifex bamboo worm	2		5/25	20.0
Characteristic of eastern 1/3 of area (A) - *Maldane* spp.				
Characteristic of western 2/3 of area (B) - Eclysippe				
Chaetopteridae				
Lumbineridae				
Minor Phyla				
Echiurida - Listriolobus hexamyotus	4		4/25	16.0

Source: (Jones and Fauchald, 1976).
[a]The characteristic species of this zone.
[b]Common by direct inspection.

Table III.B-37

DOMINANT BENTHIC INVERTEBRATES OF THE DEEP-WATER FAUNA (Z = m to 652 m) ASSEMBLAGE AT HUNTINGTON-LAGUNA BEACH HIGH DENSITY SAMPLING AREA (JONES AND FAUCHALD, 1976)

	Abundance Rank Sub-group		Abundance Mean No./ Site Sub-group		Frequency Rank Sub-group		Frequency Value Sub-group		Frequency Percent Sub-group	
	A	B	A	B	A	B	A	B	A	B
Echinodermata										
[a]*Brissopsis pacifica* sea urchin	-	-	-	-	-	-	-	-	-	-
[a]*Myxoderma platyacanthum* starfish	-	-	-	-	-	-	-	-	-	-
Crustacia										
Eurycope californiensis ispod	9	7	0.7	0.6	4	8	7/19	2/11	36.8	18.2
Campylaspis rubromaculata cumacea	18	17	0.2	0.1	13	15	3/19	1/11	15.8	9.1
Mollusca										
Mitrella permodesta snail	3	2	1.7	1.8	1	2	14/19	7/11	73.7	63.6
Tindaria californica clam	4	2	1.3	1.8	3	5	8/19	4/11	42.1	36.4
Mysella compressa clam	7	1	0.7	2.6	7	1	1/19	4/11	5.3	36.4
Polychaeta										
Maldane glebifex	1	-	4.2	-	7	-	5/19	-	26.3	-
Maldane sarsi	2	-	2.2		9	-	4/19	-	21.0	
Eclysippe vanelli	5	-	1.2	-	2	-	10/19	-	52.6	-
[a]*Nephthys cornata franciscana*										
Flabelligerida										
Spionidae										
Eclysippe vanella	-	4	-	1.4	-	1	-	7/11	-	63.6
Maldane sarsi	-	6	-	0.7	-	10	-	2/11	-	18.2
[a]*Anobothrus* sp.										
[a]*Tauberia aculata*										
Paraonidae										
Ampharetidae										
Pilargidae										

[a]Common by visual inspection.

Table III.B-38

DOMINANT BENTHIC INVERTEBRATES OF THE BANK TOP ASSEMBLAGE AT TANNER-CORTES BANK HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
Crustacea					
Clythrocerus planus decapod	3	1.4	2	14/32	43.8
Amphelisca cristata amphipod	4	0.9	1	14/32	43.8
Photis californica amphipod	6	0.8	22	5/32	15.7
Adroides columbae amphipod	7	0.7	3	12/32	37.5
Hemilampros californica cumacea	10	0.6	4	11/32	34.3
Isaeidae					
Gammeridae					
Aoridae					
Mollusca					
Micranellum crebricinctum snail	2	1.7	7	10/32	31.1
Glycymeris corteziana clam	13	0.4	9	9/32	28.1
Huxleyia minuta clam	40	0.1	37	2/32	6.2
Parvilucina tenuisculpta clam	5	0.8	16	6/32	18.8
Polychaeta					
Chloeia pinnata	1	2.1	11	7/32	21.9
Lumbrineris acuta	15	0.3	6	10/32	31.1
Syllidae					
Sabellidae	Families having greater abundance on bank tops				
Glyceridae					
Thalenessa spinosa	14	0,4	5	11/32	34.3

7

Source: (Jones and Fauchald, 1977).

Table III.B-39

DOMINANT BENTHIC INVERTEBRATES OF THE BANK-TROUGH ASSEMBLAGE AT TANNER-CORTES BANK HIGH DENSITY SAMPLING AREA

	Abundance		Frequency		
	Rank	Value Mean No./ Site	Rank	Value	Percent
Echinodermata					
Amphipholis squamata brittle star	2	3.5	17	8/29	27.6
[a]*Amphiodia urtica* brittle star	3	3.3	1	24/89	82.8
Dougaloplus amphacantha brittle star	4	1.3	5	14/29	48.3
Crustacea					
Urothoe varvarini amphipod	6	1.1	3	16/29	55.2
Ampeliscidae amphipod					
Phoxocephalidae amphipod					
Oedicerotidae amphipod					
Haustoriidae amphipod					
Mollusca					
[a]*Lima subauriculata* clam	18	0.5	21	8/29	27.6
[a]*Tomburchus redondoensis* clam	19	0.5	12	10/29	34.5
[a]*ahtoderma* sp. aplacophora					
Polychaeta					
Chloeia pinnata	1	6.5	2	17/29	58.6
Prionospio malmgreni	5	1.3	4	15/29	51.7
Praxillella affinis pacifica	7	1.0	6	14/29	48.3
Scalibregma inflatum	8	1.0	7	14/29	48.3
Paraonidae collected only in trough					
Oweniidae					

Source: (Jones and Fauchald, 1977).

[a]Common by visual inspection.

APPENDIX
Table I
MOST FREQUENT BENTHIC INVERTEBRATES OF SANTA ROSA HDSA

I Central Zone

Group A Depth $\bar{x}$ = 50 m

	Abundance		Frequency		
	Rank	Mean No./ Area	Rank	Value	Percent
Photis californica C-amphipod	1	59.4	1	7/7	100.0
Photis lacia C-amphipod	2	23.3		6/7	85.7
Amphipholis squamata E-brittle star	3	16.7	1	7/7	100.0
Owenia collaris Polychaeta	4	12.9		2/7	
Anaitides sp. a	5	8.0		6/7	
Adroides columbiae	6	8.0		3/7	42.9
Pagurus setosus C-decompoda crab	7	6.4	1	7/7	100.0
Spiochaetopterus costarum Polychaeta	8	6.0	1	7/7	100.0
Amphipholis pugetana E-brittle star	9	5.6		6/7	
Idarcturus allelomorphus	10	5.4		6/7	
Peisidice aspera	12	4.7	1	7/7	100.0
Lumbrineris sp.	13	4.6	1	7/7	100.0
Crenella divaricata	25	2.3	1	7/7	100.0

+ 6 more spp. occurring 6 times.

Source: Jones and Fauchald, (1977).

Group B Depth $\bar{x}$ = 77

	Abundance		Frequency	
	Rank	Mean No./ Group	Rank	Value	Percent
Photis lacia	1	27.4	1	7/7	100
Euphilomedes carcharondonta	2	19.6	1	7/7	100
Amphipholis squamata	3	10.3	1	7/7	100
Parvilucina tenuisculpta	4	8.0	-	5/7	71.4
Micranellum crebricinctum	5	5.9	-	4/7	57.1
Drilonereis falcata	21	2.0	1	7/7	100
Lumbrineris sp.	7	4.3	5	6/7	85.7
Ampelisca pugetica	8	3.6	5	6/7	85.7
Adroides columbiae	14	2.9	5	6/7	85.7
Clavopora occidentalis	16	2.7	5	6/7	85.7
Pargurus setosus	22	2.0	5	6/7	85.7
Pholoe glabra	24	1.9	5	6/7	85.7

Group C
Depth $\bar{x}$ = 102 m

	Abundance		Frequency	
	Rank	Area Mean No./ Site	Rank	Value	Percent
Ophiopholis bakeri	1	13.8	1	4/5	80.0
Peisidice aspera	2	2.2	1	4/5	80.0
Ampelisca lobata	3	1.6	1	4/5	80.0
Amphipholis pugetana	4	1.2	1	4/5	80.0
Hiatella arctica	5	1.0	-	2/5	40.0
Liljeborgia cota	6	1.0	-	1/5	20.0
	Z $\bar{x}$ = 103 m Central Group D				
Euphilomedes carcharondonta C-ostracod	1	27.3	1	12/12	100.0
Adroides columbiae	2	7.2	1	12/12	100.0
Photis californica	3	5.6	-	7/12	58.3
Amphipholis squamata	4	4.9	6	11/12	91.7
Pardisynopia synopiae	5	4.8	1	12/12	100.0
Photis lacia	6	4.2	7	9/12	75.0
Chloeia pinnata	7	3.1	-	4/12	33.3
Byblis veleronis	8	3.1	1	12/12	100.0
Clythrocerus planus	8	3.1	1	12/12	100.0
Sthenelanella uniformis	11	2.0	8	8/12	66.7
Urothoe varvarini	10	2.5	8	8/12	66.7
Brilonereis falcata	-	0.8	7	9/12	75.0

Group E
Depth $\bar{x}$ = 108 m

	Abundance		Frequency	
	Rank	Mean No./ Group	Rank	Value	Percent
Euphilomedes carcharondonta C-ostracod	1	11.8	4	8/10	80.0
Amphipholis pugetana E-brittle star	2	10.3	1	10/10	100.0
Amphipholis squamata E-brittle star	3	9.1	1	10/10	100.0
Ophiopholis bakeri	4	5.0	9	6/10	60.0
Photis californica C-amphipod	5	4.3	9	6/10	60.0
Pardisynopia synopiae	6	3.4	3	9/10	90.0
Adroides columbiae	17	1.2	4	8/10	80.0
Terebellides stroemii	15	1.4	4	8/10	80.0
Pagurus setosus	17	1.2	7	7/10	70.0
Perisidice aspera	10	2.0	7	7/10	70.0

I Peripheral Zone

Group F Depth = 162 m; 26 m to 327 m

	Abundance		Frequency		
	Rank	Mean No./ Group	Rank	Value	Percent
Parvilucina tenuisculpta	1	18.0	2	13/14	92.8
Mysella tumida	2	13.2	-	2/14	14.3
Ampelisca macrocephala	3	5.1	-	5/14	35.7
Lumbrineris sp.	4	4.6	1	14/14	100.0
Tellina carpenteri	8	3.5	2	13/14	92.8
Drilonereis falcata	-	1.3	4	11/14	78.6
Amphiodia urtica	-	2.4	5	10/14	71.4
Pectinaria californiensis	-	1.4	5	10/14	71.4
Prionospio near *malmgreni*	-	1.7	5	10/14	71.4
Pardisynopia synopiae	-	1.6	8	9/14	64.3
Choeia pinnata		-	-	5/14	35.7
Group G Depth $\bar{x}$ = 234 m					
Chloeia pinnata	1	7.0	4	6/10	60.0
Parvilucina tenuisculpta	2	5.1	-	4/10	40.0
Huxleyia minuta	3	3.7	2	7/10	70.0
Tellina carpenteri	4	3.4	4	6/10	60.0
Adroides columbiae	5	2.6	1	9/10	90.0
Urothoe varvarina	-	1.8	2	7/10	70.0
Amphipholis squamata	-	1.7	4	6/10	60.0
Euphilomedes carcharondonta	6	6.4	4	6/10	60.0
Lumbrineris sp.	13	1.2	4	6/10	60.0
Ampelisca macrocephala	8	1.9	-	5/00	30.0

C. Rocky Shore Intertidal Communities: Southern California Bight

Introduction. The first part of this section will present an introductory summary of the principal environmental factors governing the distribution of rocky shore intertidal organisms and some of their biological adaptions to these environmental factors. A brief discussion of succession will be included. The introduction will be followed by a coverage of the intertidal communities of some specific areas and some reproductive aspects of individual species comprising these communities. Much of the work has been done in central California and the majority of examples illustrating these principles comes from these locations.

There are many environmental conditions which affect the distribution and abundances of intertidal organisms and communities. In reality these factors interact with each other all at the same time with the fluctuating magnitudes of certain factors causing the importance and magnitude of the others to similarly fluctuate (sometimes in unknown ways) in response. To separate these influences and discuss them alone, therefore, tends to oversimplify the situation and to present a mosaic rather than a clear, complete picture. Something as complex as ecology can often be understood and analyzed if dissected into its individual though overlapping components.

In order to have a rocky shore intertidal community, there must be a coastline having the proper overall environmental conditions. This would lead one to consider the biogeographical factors which have influenced the establishment of the intertidal populations. The area must have a coastline of proper substrate upon which individuals of the community may settle. The species occupying the habitat have had a long history of evolution which has adapted them to their environment. Temperature is often considered one of the most important environmental variables governing the species composition of a geographical area. Other factors such as geographical isolation also preclude the presence of certain species. For example, many Atlantic coast species which could survive on the California coast are absent because of the continental barrier between the two oceans. Nonetheless, several Atlantic coast species which have been introduced on the Pacific coast have become established on California coasts (Keen, 1937).

Other important factors which govern the geographical distribution of intertidal organisms are salinity (generally near to sea water in the outer coasts of California), currents as they influence larval spreading and setting, food (plankton and detritus), and other physiologically important factors such as dissolved oxygen and dispersal of biological wastes and sediments.

Much remains to be understood about intertidal ecology both in general and in California in particular. Because of the excellent work done by the faculty and advanced degree students over a period of over 30 years at

Hopkins Marine Laboratory at Monterey Bay, the intertidal biology of this area is perhaps one of the best known in the country.

Even in Monterey Bay, directly off the Hopkins Marine Laboratory, thorough studies can produce unexpected results. Glynn (1966) selected for extensive studies a narrow band dominated by a red algae and barnacle on the high intertidal, partly because he believed it to be a simple community containing only a few well known species. He found this association to contain over 90 species, of which five were completely new to science and two common species represented range extensions for organisms previously reported to occur only in the Sea of Japan and Europe.

According to Hedgpeth in Ricketts, et al., (1968), several basic factors not understood about intertidal communities are the almost geometrical cutoff of zones in some places, with bare, unoccupied space above or below; the alternation between zones of plants and animals often observed in the upper parts of the intertidal region. Another very basic question is the effect of increased velocity of the tidal current during the middle of the tidal cycle. Observing the establishment of organisms on concrete slopes of a new seawall, Moore and Sproston (1940) found that the middle zone, most subject to the swifter tidal currents, was the last to reach the climax condition, whereas the extremes developed first.

Of the many environmental factors influencing the distribution, composition, and abundance of intertidal organisms Ricketts, et al., (1968) listed wave shock or surf, substrate, and exposure as the most important. The most obvious factor from casual observations of an intertidal area is the vertical distribution of the organisms which often seem to form distinct associations. Generally, the upper area contains only a few species which appear to be transitional between land and sea forms. These organisms can survive neither completely on land nor completely in the sea. The upper area grades into lower areas having more and more species occupying more and more of the available space until somewhere around mid-level every conceivable space is inhabited by algae or invertebrates. Most, although not necessarily all in every circumstance, environmental factors mentioned below influence the vertical distribution and zonation of intertidal organisms.

According to Stephenson and Stephenson (1972), who have studied numerous intertidal areas around the world, there is a vertical zonation common to all areas, being absent only in areas where exceptional conditions have modified these common features so much that they are not easily recognized in their changed form. Some conditions, such as polar ice, can suppress the common characteristics altogether.

The Stephensons recognized three principal zones, a *Littorina* (periwinkle) zone above, a barnacle zone in the middle, and a wetter zone of variable population below. Additionally, there is typically a blackish myxoplycean (a lower fungus) or lichen zone at a high level, and an incrustation of

lithothamnia (coralline algae) over the lower parts of the rock. MacGinitie (1939) also recognized three vertical zones in Monterey Bay. Although Hedgpeth in Ricketts, et al., (1968) indicated agreement that the intertidal was divisable into three parts, he indicated the fallacy of considering a zone of algae in one part of the world and a zone of ascidians (tunicates) at the same tidal level in another part of the world as ecological equivalents. Vertical zonation will be discussed in more detail below.

Tides. Tides are the principal governor (although waves are also important and can greatly modify the effect of the tides) of the amount of exposure and submergence intertidal organisms experience. The tides of California are termed mixed semi-daily tides consisting of two high tides and two low tides of unequal amplitude a day (Figure II.C-1). In terms of the intertidal, the highest levels 1.3 to 1.9 m (4.5 feet to 6.5 feet) are submerged only once a day while the lowest levels -0.45 to +0.45 m (-1.5 to 1.5 feet) are exposed only once a day. This is contrasted with the middle levels 0.5 to 1.3 m (1.5 to 4.5 feet). Many of the other areas throughout the world which are exposed and submerged twice a day (England, for example) have essentially equal diurnal tides and are similarly exposed and submerged two times a day. It would stand to reason that this added variable at areas having mixed tides would cause additional or more discrete vertical zones than at areas having equal tides. Ricketts, et al., (op cit) reported that a number of workers have noticed more discrete zones at areas like California having mixed tides.

In addition to the daily tidal fluctuation, the amplitudes of tidal ranges vary with the phases of the moon. Every lunar month (28 days) there are two periods having maximum tidal amplitudes (spring tides) and two periods having minimum tidal amplitudes (neap tides).

Organisms of the intertidal are, with few exceptions, of marine origin. This is to say that, even those species that are fairly well restricted to the intertidal and those which spend nearly all their time exposed to the air, are derived from marine ancestors and their closest relatives are marine. Further, extended periods of exposure will cause desiccation and death to most of these organisms. Because of this danger, both the length of exposure time and the climatic conditions when exposure occurs are important to the survival of members of the intertidal community. Periods of hot, low humidity, and windy weather with mid-day sunshine and little cloud cover enhance dessiccation. The opposite weather conditions tend to retard desiccation and generally assist survival. To complicate matters further, however, often increased precipitation accompanies these weather conditions causing decreased salinity, particularly in intertidal pools. Low salinity, particularly as it approaches fresh water, puts a stress on intertidal organisms which can cause death.

The low tidal periods in California are generally favorable to intertidal organisms (Hewatt, 1937; Glynn, 1966; and Stephenson and Stephenson, 1972).

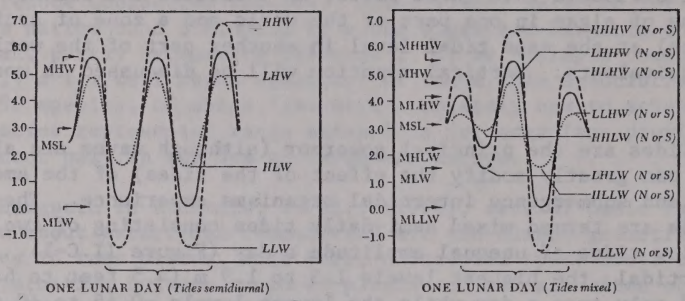


Figure III.C-1 Types of tidal curves, after Doty. Solid line = mean range of tides; broken line = maximum range; dotted line = minimum range.

Source: Ricketts, et al., 1968.

Substrate and Topography. The fact that intertidal biota is divided into that living on rocky substrate and those which are not, both in this narrative and nearly all other papers and texts, certainly attests to the importance of this substrate in contrast to a soft bottom substrate. An essential difference among benthic organisms is that some are able to attach to and live on (epifauna,-flora) a hard rocky substrate, while other species find a better survival adaptation by living in, rather than on (infauna) a soft sand or mud bottom. Even the composition of the rocky substrate can influence the type of organisms which live there. For example, Stephenson and Stephenson (op cit) reported this effect on sandstone at La Jolla, California:

> The rock colonised by the intertidal organisms is of a curious type. Most of it is sandstone, and of this, the greater part is relatively soft. At its softest, one can rub down the surface of the rock with a fingernail or remove it easily with a knife. But from one small area to another, the consistency varies, and in some places, there are tracts of sandstone that are much harder. In many places, small concretions, boulders, or eminences of hard rock are inset in the softer sandstone, so that it is possible to make a direct comparison of the population of one of the hard insets with that of the surrounding softer rock at the same level. The soft rock, being too friable, forms a poor surface for the attachment of barnacles; but at the same time, it is porous and absorbs sea water, so that it retains moisture in its superficial layers when the tide has receded, which enables lithothamnia to encrust it to levels at which they would otherwise die from desiccation. Conversely, the hard rock, which dries off readily and discourages lithothamnia at such levels, is heavily colonised by barnacles. Apart from the sandstone, there are seams and areas of shale, which also vary in hardness. In some places, the soft shale is riddled by boring bivalves, such as *Petricola californiensis* and *Pholadidea penita*. Conglomerate also occurs locally.

The subject of the rocks of the intertidal area is another variable which affects the composition of the community. Generally, when one refers to rocky shores it is understood that the majority of the substrate is an exposed portion of a solid permanent geologic structure, such as a rock outcrop, having a relatively long existence at that place. In addition to the solid rock foundation, there are varying amounts of large boulders which are resistant to all but the largest storm waves. These boulders together with cracks and crevices in the basal rock provide a special under-rock habitat for invertebrates where only certain species are found in large numbers (Ricketts, et al., 1968). Certain beaches are comprised of boulders. Due to the seasonal deposition and erosion of sand and the frequent to rare movement of the boulders by wave action, this habit may be subject to far greater fluctuations than a solid rock area, but does provide substrate and protection for intertidal organisms.

The slope of the rocky area is also very important. A vertical cliff intertidal community will have different characteristics than one on a sloping surface. An extensive flat area, such as Duxbury Reef north of San Francisco, will be somewhat different from the other two. The relationship of the slope, or overhang, to sunlight, is still another variable and can particularly affect the distribution of algae and algal grazers.

As indicated above, large boulders and cracks and crevices provide protection and shelter for many species. Protection and shelter are also provided by sessile organisms, such as mussels, barnacles and algae even on flat surfaces where cracks and crevices are rare.

Waves and Surf. According to Ricketts and others the degree of wave shock in the Pacific is of particular importance. According to the physics of wave motion, the size of the continuous water area (fetch), wind velocity and wind direction determines the size of waves. The great expanse of the Pacific Ocean makes fetch important in comparison with the Atlantic or Gulf coasts. When, in addition, there is a bluff, unprotected coast with few islands or high submarine ridges for thousands of miles, as from Cape Flattery to Point Conception, with prevailing northwesterly to westerly winds, wave shock is probably more powerful than in any other part of the Northern Hemisphere.

Various factors modify the force of the waves in particular regions which cause correlative variations in the animal assemblages. The wave variation runs the gamet from the pounding surf of 6 m (20-foot) ground swells to the enclosed bays and estuaries where there is almost no surf at all. Although the latter areas are covered elsewhere, certain semi-protected areas, and areas behind man-made breakwaters and jetties nearly fit this category during the majority of the year.

Ricketts divided the outer coast into a protected coast and an open coast, realizing the communities can show a great deal of overlap, particularly where the amount of wave shock grades into the other category.

The protected outer coast consists of what could be considered semi-sheltered coast and open bays where the force of the surf is somewhat dissipated. These shores are generally concave, and are characteristically protected by a headland or a close-lying island (Figure III.C-2). Santa Barbara, much of Monterey Bay, Half Moon Bay, Bodega Bay, Arena Cove, Shelter Cove and Trinidad Bay are good examples. Stretches of shore that first appear to be entirely open to the sea may actually belong to this category. An offshore reef of submerged rocks or a long gradually sloping strand is sufficient to break the full force of the waves and will greatly modify the character of the intertidal assemblages. Even distinct headlands, outlying bars, or offshore islands, if they are in the direction of the prevailing winds, provide a degree of protection that makes the assemblage correspond to the protected outer coast category. An offshore kelp bed will serve the same purpose, smoothing out the water to such an

extent that boats often seek shelter inside the beds. In many places the protection is indirectly due to headlands' and offshore rocks' refraction of waves (Figure III.C-3). Because waves tend to approach parallel to the shore, they tend to bend around a headland, meeting it headlong from all sides. The substrate of a protected open coast can either be rocky shores or sandy beaches.

The entirely unprotected, surf-swept shores of open coast has by no means as rich a community as a protected shore, but does support a distinctive and characteristic group of organisms which either require heavy surf or have adapted to tolerate it. This type of shore is usually convex (Figure III.C-3), varying from bold headlands to gently bulging stretches, and there will be fairly deep water close offshore. Pismo Beach, the Big Sur and Point Lobos outer rocks, and the outer reefs of Cypress Point and Point Pinos are all good examples from the central California coast. Most of the coast of northern California falls into this category. Most of the coastline of Southern California is of the semi-protected type due to the Channel Islands. Several windows are present, which allow the mainland coast to receive severe wave shock (e.g. Ocean Beach near San Diego). The outer shores of the Channel Islands are generally exposed.

The vertical distribution of intertidal assemblages is greatly modified by the size of the waves, as the zones are not fixed according to tidal levels but tend to spread wider and higher toward the region of heavier wave action (Figure III.C-4). This is often particularly evident on exposed coasts, along a vertical face set at right angles to the main direction of the waves; the zones will be wider than in protected areas. In very sheltered regions the whole zonal pattern may be lowered so that the uppermost zone is actually below the highest watermark of the year.

Waves may combine with other physical factors to erode and transport sediment from sandy areas and deposit it on a rocky intertidal area. Certainly this, whether seasonal or constant, modifies the composition and decreases the abundance of the intertidal community (Nicholson and Cimberg, 1971).

It should be apparent that with all the variations in coastal configurations over small areas, it would be unrealistic to conceive of long stretches of rocky coastlines as having identical intertidal assemblages; rather, it is more realistic to perceive the assemblages as occurring as small patches. Although given similar substrate, wave shock and tides, the other variables mentioned in this section would tend to cause assemblages in different locations to differ in detail, some highly significant and important, although the general overall characteristics would be very similar.

Temperature and Sunlight. In addition to being one of the main factors governing the geographical distribution of organisms, temperature can also play an important role in influencing microhabitats. Heat can kill intertidal organisms either directly (Goltstoff, 1964) or by increasing the

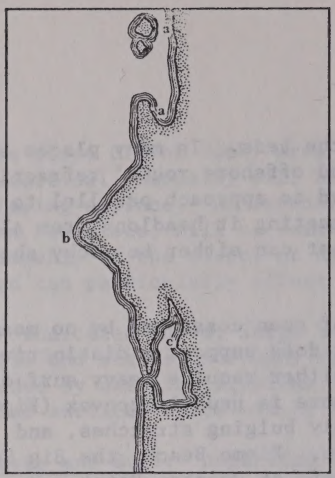


Figure III.C-2 Types of coastline: *a*—*a* is a typical stretch of protected outer coast; *b*, a characteristic headland on the open coast; *c*, an enclosed bay and estuary.

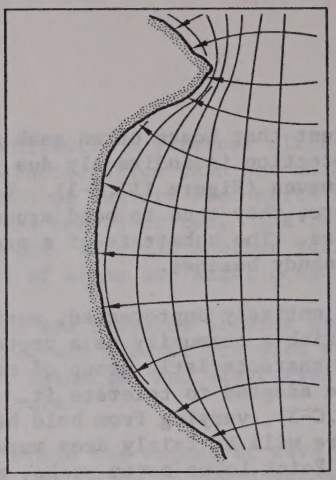


Figure III.C-3 Wave refraction on an irregular shore. A beach need not be in the lee of an offshore feature to be protected from heavy wave action.

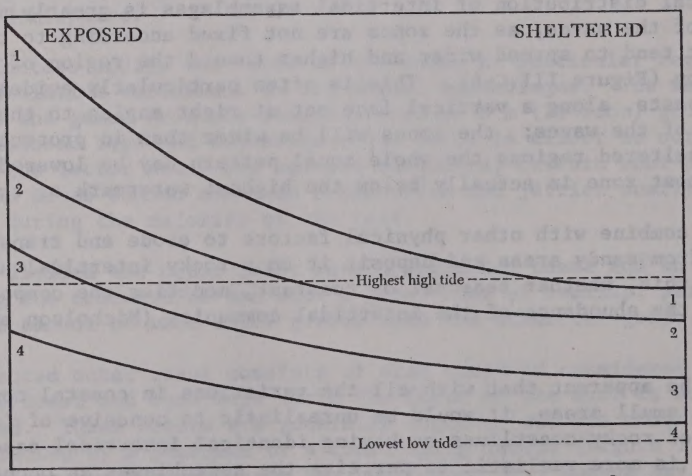


Figure III.C-4 The zones are displaced upward as one proceeds toward the more exposed part of the coast; such a displacement is often seen on rocky headlands. This is a schematic diagram, and it is not intended to indicate actual height.

Source: Ricketts, et al., 1968.

rate of desiccation. Bare rock exposed to direct sunlight absorbs most of the sun's energy causing it to become extremely hot. Algae and other plants absorb significant quantities of the energy, much of which is used in the endothermic photosynthesis reaction. Glynn (1966) measured an 8°C difference between the air temperature just above an exposed bare rock and the shadowed interior of a tuft of the red algae *Endocladia muricata* when the official air temperature was around 30°C. Sunlight has been shown to influence the vertical dimensions of intertidal zones in areas of negligible surf or tides (Ricketts, et al., op cit).

The rate of temperature change can be important to the welfare of intertidal communities, subjecting its members to greater stresses with more rapid diurnal temperature fluctuations. The same relationship exists with seasonal variation. California water temperature fluctuation is favorable for the establishment and survival of rich communities, with the mean monthly temperatures fluctuating 8°C (46.4°F) or less (see Temperature section). At Monterey Bay, Glynn (1966) recorded the extreme water temperature range during his three-year study to be 6°C (46.4°) 10.5° to 16.5°C (50.9° to 61.7°F). The temperature range is less in northern California than in Southern California because the upwelling period brings cold water to the surface during the summer when air temperatures would otherwise cause a greater water temperature increase.

Exposure. As suggested above, exposure is probably the critical limiting factor to the vertical location of intertidal organisms. The adaptations to air exposure vary with the species and include many, often complex, physiological, morphological and behavioral modifications. Some species (*Littorina* spp. and many limpets) are specially adapted for extended periods of exposure and cannot survive long periods of submergence, while others (many acorn barnacles - *Balanus* spp.) can flourish in a wide vertical range but are largely confined to the more exposed regions because they are out-competed by other plants or animals in the lower regions.

The critical vertical level of most intertidal organisms is largely dependent upon exposure, but opinions on the critical limiting aspects of it vary. Ricketts considered the average period of exposure (based on cumulative exposure over six months) and noted a striking difference on either side of the 1 m (3.5 feet) level which corresponded to an exposure of under 50 percent of the time in a 6-month period, and where the maximum single exposure below this level is only half as long as the exposure immediately above it (Figure III.C-5). Hewatt (1937), using the same technique, reported the largest change occurred on either side of the 0 m (0-foot) datum where Monterey Bay intertidal organisms were exposed less than 10 percent of the time.

Roberts (1941) believed that the duration of a single exposure to have greater moment than the sum of numerous exposure periods. Figure III.C-6 shows the longest single tidal exposure at different vertical levels and indicates a sharp break in the curve occurs between 0.75 to 0.9 m (2.5 and 3.0 feet). This level corresponds with the height of low high tide. On coasts of the eastern Pacific having mixed tides, organisms located below

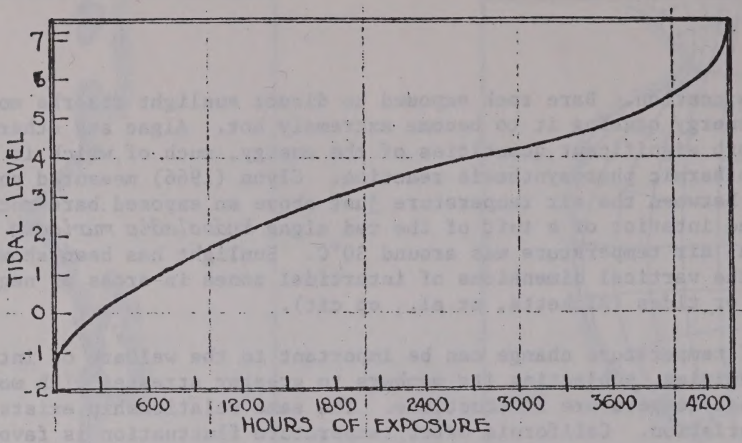


Figure III.C-5 Graph of total exposure for six-month period, January 1 to July 1, 1931 (from Hewatt, after Ricketts).

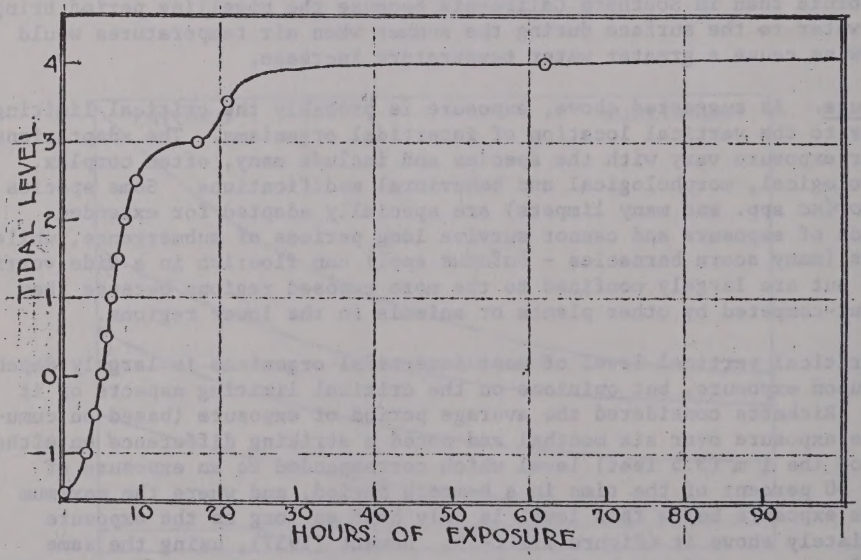


Figure III.C-6 Graph showing the longest single tidal exposure at each 0.5 foot interval at Monterey during the period January 1 to July 1, 1941.

Source: Roberts, 1941.

low high waters are submerged (during low high waters), while organisms located above this level remain exposed. As illustrated in Figure III.C-7, organisms below the 0.9 m (2.9 foot) level are exposed during low low water (A) and low high water (B) for periods of about nine hours and five hours respectively. Organisms above the 0.9 m (2.9 foot) level are exposed for a continuous 17-hour period represented by line C. Organisms will have to be, in terms of duration, twice as well adapted to withstand exposure to sun and wind than its neighbor only several centimeters below. This factor apparently does manifest itself in intertidal communities of California, for the height reached by the lower high water corresponds closely with both Hewatt's second zone and Rickett's semi-protected Zone 2, or high intertidal zone.

According to Roberts, the same type of situation occurs at the lower limit reached by the higher high water 1.2 m (3.9 feet). The period of longest exposure for an organism at the 1.0 m (3.5 foot) level would be 20.5 hours, while that for an individual at the 1.2 m (4.0 foot) level would be tripled, or 62 hours (Figure III.C-5). At this level only a few organisms are able to survive, but interestingly this line closely coincides with the upper limit of the barnacle *Balanus glandula* (Hewatt, 1937, Ricketts, et al., 1968 and others) as well as the *Endocladia-Balanus glandula* community reported by Glynn (1966).

These levels represented a semi-protected area where the water levels are controlled by tidal heights with very little modification by wave. At more exposed areas, the large waves are superimposed upon the tides and the zones are extended upward as indicated above.

Doty (1946) considered that the vertical distribution of algae, in particular, is correlated with the sudden increases in the maximum time of a single exposure that occur at certain parts of the tidal circle or, conversely, to sudden increases in the duration of submergence of the algae. The critical level for a species would depend upon combinations of both tide levels and short time factors. They become critical levels when they coincide with other secondary factors acting upon the organisms.

Roberts (1941) conducted studies on the methods employed by three invertebrates (*Littorina planaxis, Tegula funebralis*, and *Anthopleura elegantissima*) to resist desiccation, and summarized additional methods of other species.

Methods include migration with the falling tide. This category would include a number of fishes, such as *Scorpoenichthys* sp. and *Hemagrammes* sp. It also includes other comparatively active organisms such as starfish, nudibranchs, and some crabs.

> Another way of meeting this problem is that of selecting a permanently moist habitat. This method can be used by both sessile or free-living types. A permanent tide pool will have its population of cottid fishes, shrimps, and nudibranchs. Many sponges, bryozoans, and crabs select as a habitat the under

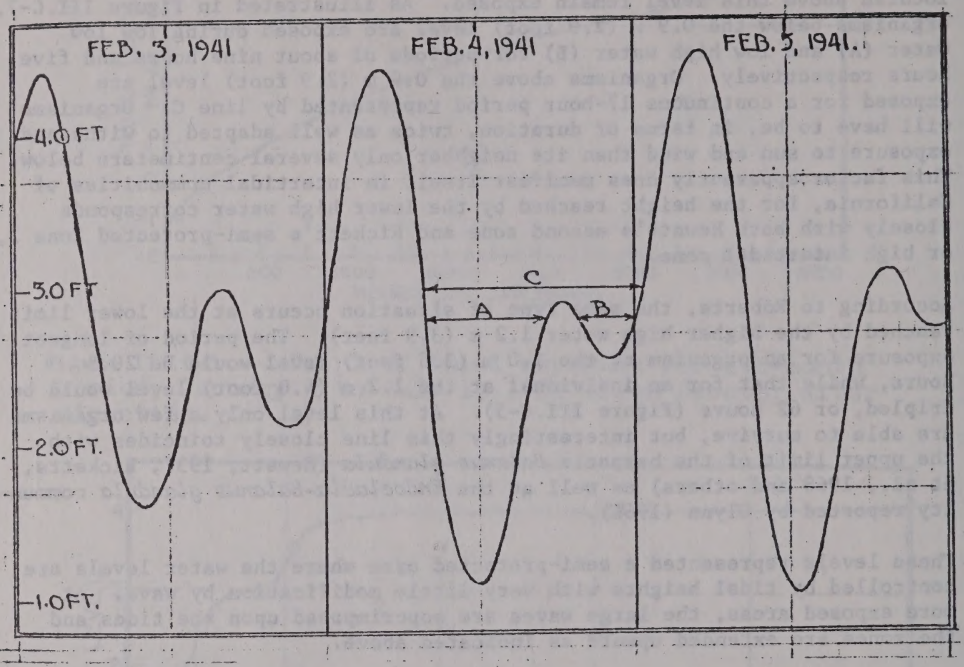


Figure III.C-7 Graph showing the tidal curve during the three day period February 3 to February 5, 1941. On February 4 the lowest of the lower high waters for the year reached an elevation of only 0.62 m (2.9 feet).

Source: Roberts, 1941.

surface of a rock ledge or shelf where there is high relative humidity during low tide and where they can derive protection from the sun and wind. Numerous worms, molluscs, and crustacea are protected from desiccation by burrowing in moist sand, rock, or wood. The snail, *Tegula funebralis*, will be found in large numbers under an algal curtain where moist conditions prevail.

Organisms, such as the anemone, *Anthopleura elegantissima*, aggregate into groups for protection against desiccation and at the same time give protection to other forms, such as worms and pycnogonids which live between the crowded individuals. The manner in which anemones may reduce the evaporating surface by aggregation can be described in the following way. Let us consider a single anemone is a cube with six surfaces, attached to the substrate by its base. This leaves exposed five surfaces, the top and four sides, from which evaporation can take place. If another anemone is in contact with the original specimen, only four surfaces will be exposed to evaporation, the top and three sides. If all four sides are protected by other organisms, evaporation can take place from only one of its six faces, the top surface. Consequently, the water loss will be reduced by approximately 85%.

Some organisms may aggregate in organically connected colonies, which by their form, provide a means of holding a water film. The ostrich-plume hydroid, *Anglaophenia struthionides*, has its parallel hydrocladia spaced closely enough together to hold, because of capillary attraction, a thin sheet of water. This water far exceeds in volume that which the colony could hold if the hydrocladia were spaced far enough apart to lose the water film.

Foreign material is used by some animals as a means of protection against desiccation. Such material often serves to retain considerable amounts of water. Numerous worms such as *Thelepus plagiostoma* use debris in this manner while sand and broken shells are utilized by the anemone *Anthopleura elegantissima*.

Certain organisms are so modified in form as to provide a sealed chamber, or we might speak of it as a "cork and bottle" arrangement. The numerous barnacles, snails, tube worms, and even the limpets can be placed in this category. The opercula or opercular plates serve as the "cork" for most of these organisms, but the limpet uses the substrate to seal the opening of its shell. Limpets of the higher intertidal levels, such as *Acmaea scabra*, migrate in search of food, but during periods of exposure each one returns to its exact "home" in order to occupy the one place on the rock where its shell will fit tightly all the way around the margin.

Some organisms suspend activity during periods of exposure and stay in place on the rocks. An example is the snail, *Littorina*

planaxis, which can secrete a mucous attachment to the rock, close its operculum, and remain inactive until it is dampened by spray. Since the period of inactivity may be of several months duration, it must be assumed that metabolic activities are reduced to a minimum. These recurrent periods of inactivity are at least analogous to the hibernation of certain vertebrates.

Only active organisms can protect themselves from desiccation by migration but all of the other foregoing methods can be used either by sessile organisms or by free-living types. One particular species may use several methods at the same time. The snail, *Tegula funebralis*, a "cork and bottle" type of organism, can migrate to a permanently moist habitat under an algal curtain and there aggregate and also hibernate until the time of the returning tide.

Shelter. The protection, from desiccation and predation by forming a place to hide, and increased substrate provided by larger sessile organisms changes both the composition and abundance of the community in comparison with bare rock areas by allowing certain species to live at a higher vertical level.

The mussel bed gives an obvious illustration of an organism providing a habitat which allows the presence of certain organisms and an increase in the abundance of others. Examples of important organisms typical of mussel beds which could not live at the various levels occupied by the mussel zone or on bare rock are the little flat crab *Petrolisthes cinctipes*, the isopod *Cirolana horfordi* and the worm *Merlis vexillosa* (Ricketts et al., 1968). The dense growth of mussels provides shelter for them and the spaces between the mussels and their byssal threads (attachment structures produced by the foot of the mussel) serve as traps for detritus on which some associates feed. As the bed grows, more and more crevices and sheltered spots are developed beneath and between the shells until some animals, like the sipunculid worm and sea cucumbers, which usually live under rocks in sheltered places nearer shore, find habitats in the mussel bed.

MacGinitie (1939) emphasized the increase of food and/or increased food-obtaining abilities provided by mussels. For example, the isopod *Carolana hardfordi* is a scavenger, living on dead or decaying flesh. The population of *C. harfordi* reaches its greatest abundance on mussel beds because mussels not only smother each other out, and this affords a certain amount of food material, but the bed also acts as a trap for food which is destroyed in the plankton along shore by the heavy surf. Although seaweeds and rock crevices also furnish such a trap, *Cirolana* does not occur as abundantly as in a mussel bed, because the latter provides a greater amount of refuge space than does an equal amount of rocky region. The food settling out of the water falls or is wedged into the spaces between the mussels where the flow of water is at a minimum and where, consequently, *Cirolana* can best avail itself of it.

The crab *Petrolisthes cinctipes* is a plankton feeder which by virtue of its protected location under and between mussels would appear to be involved in the competition for plankton with the plankton feeding mussels. However, *Petrolisthes* benefits from the protection through increased feeding efficiency. It is able to move out nearer the surface of the bed when the tide is in, and when the surf is not too heavy, obtain its supply of food.

Thais emarginata is a predacious gastropod. It attacks thin-shelled molluscs, and therefore exerts a great deal of influence on the small mussel crop. It cannot, however, occur in very great numbers until the mussels are large enough to afford it protection. It cannot prevent the original set of mussels during establishment or reestablishment of the community to any great extent, for to do so would prevent the survival of its own population.

Mussels not only alter the physical environment, the substrate on which they settle, they also affect the water by extracting plankton and detritus from it in tremendous quantities.

Straughan and Kanter (1977) conducted a detailed survey of the mussel community throughout the California Bight area which will be discussed below.

The mussel bed is not, of course, the only significant community on the rocky shore. There are many others, and even an apparently insignificant association of organisms may involve appreciable amounts of energy and a standing crop (or "biomass") of organic matter. For example, there are the tufts of the red alga *Endocladia* that are found interspersed with *Balanus glandula* on the rocks above the *Mytilus* zone. This *Endocladia muricata-Balanus glandula* association (Figure III.C-8) was studied for some years at Pacific Grove by Peter Glynn (1966). He found 93 species of plants and animals in this association, but only 28 of the animal species occurred more than 98 per cent of the time. Of these, a small viviparous clam, *Lasaea cistula*, found only in this association, was among the most abundant, sometimes occurring by the thousands in comparatively small areas. In the most concentrated part of the zone Glynn found more than 210,000 individuals per square meter, representing a total dry weight of 2,640 grams per square meter (roughly equivalent to 5 pounds per square yard). This elaborate microcosm thrives in a zone that is under the sea only 28 percent of the time and accordingly receives suspended food material from the sea in lower amounts than organisms at lower vertical levels.

Food. Feeding or nutrient-procurement types on rocky intertidal areas can be divided into autotrophic macrophytes - the larger attached algae: autotrophic algae and heterotrophic bacteria forming a thin film on the hard surfaces; filter feeding animals; herbivores; carnivores; and omnivores and scavengers.

The relative importance of the feeding types depends upon the vertical zone and the particular assemblage involved. In comparison with soft

Figure III.C-8 Spatial arrangement of some of the more common species in the *Endocladia-Balanus* association. The relative quantities of organisms shown at the top are proportional to those found in a test patch. Lower left: interior of two empty *Balanus* shells. Lower right: an enlarged thallus of *Endocladia muricata*.

Source: Glynn, 1966.

bottom communities the most distinctive feeding type of rocky substrate is the scraping and grazing herbivores. Although unique, their relative importance appears to be somewhat less than that of filter-feeders. Glynn (1966), for example, indicated herbivores were, in terms of biomass, only about 20% as abundant as filter-feeders.

> Analysis of the association in terms of the protein content of the standing crop of the major trophic groups shows the following: filter-feeding animals, 84 g/m^2; larger red algae and their attached epiphytes, 58 g/m^2; resident herbivores, 12 g/m^2; transient herbivores, 1.2 g/m^2; resident carnivores, 0.9 g/m^2; transient carnivores, 0.8 g/m^2; omnivores and scavengers, 1.3 g/m^2. Although the scraping and grazing herbivores feed on algae produced in the zone, much of the food consumed in the association is derived by importation of suspended detritus and plankton at high water.

Much of the material consumed by filter-feeders may be suspended or particulate organic matter, much of which was originally produced by intertidal communities.

> The plankton and other material suspended in the water present during high tide periods was sampled and analyzed at weekly intervals for a 14-month period. These pelagic materials, in order of decreasing absolute volume, were: (a) large plant fragments; (b) phytoplankton; (c) other organic detritus; (d) zooplankton; (c) inorganic detritus. Large plant fragments, composed mainly of algae and *Phyllospadix*, were abundant throughout the year and made up more than 50% in absolute volume of the samples except in June and July. The absolute volume of phytoplankton and zooplankton was noticeably higher in the spring and summer months. On a yearly basis, approximately 570 mg dry weight of suspended materials are available per m^3 of sea water.

The food web of a mussel bed is illustrated in Figure III.C-9 and that for the *Bolanus glandula* - *Endocladia muricata* community, by Glynn in Figure III.C-9a.

Communities. Rocky shore intertidal communities are integrated communities of plants and animals where the organisms are interdependent upon nutrients, food, shelter and attachment substrate.

Some of the earlier opinions of intertidal associations were formulated by zoologists or botanists who often underestimated the role of the other "kingdom" to the community. Although MacGinitie (1939) realized the importance of algae for cover, his opinion of the role of plants has not been confirmed by the subsequent work of Glynn, Stephenson and Stephenson, and others.

> I do not believe that the seaweeds should be afforded a very important place in marine animal communities, because the influence which they exert on a marine animal community is

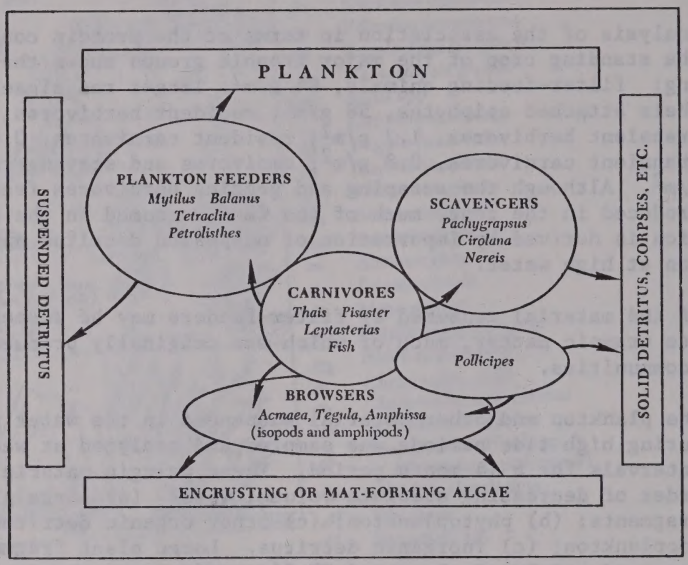


Figure III.C-9 **The food chain in a Pacific coast mussel bed.**

Source: Ricketts, et al., 1968.

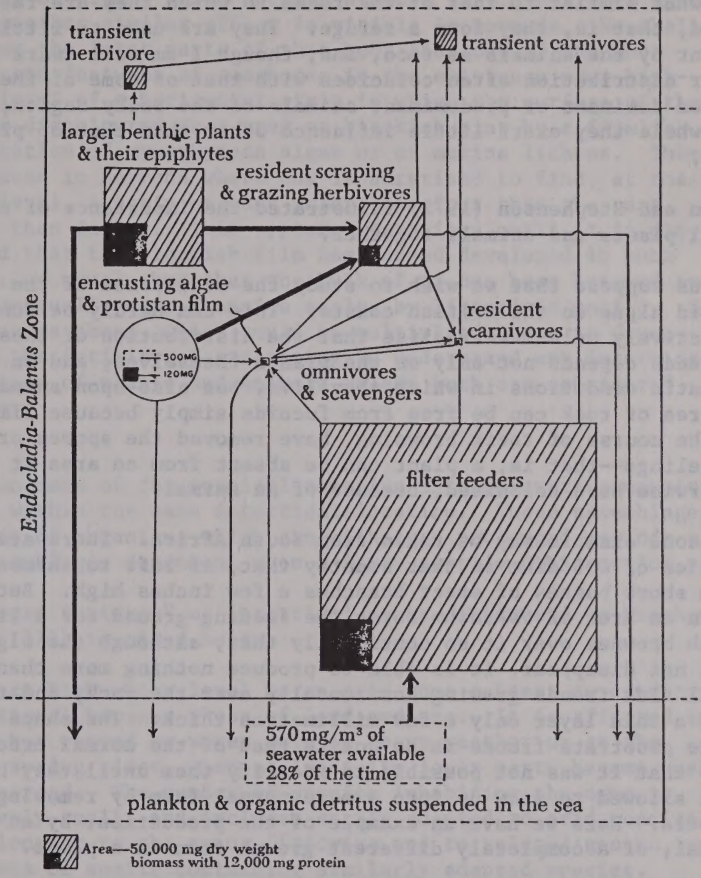

transient herbivore
transient carnivores
larger benthic plants & their epiphytes
resident scraping & grazing herbivores
encrusting algae & protistan film
500MG
120MG
resident carnivores
omnivores & scavengers
filter feeders
Endocladia-Balanus Zone
570 mg/m³ of seawater available 28% of the time
plankton & organic detritus suspended in the sea
Area—50,000 mg dry weight biomass with 12,000 mg protein

Figure III.C-9a Diagram showing average dry weight biomass and protein content of the organisms of the *Endocladia-Balanus* association, grouped in categories according to food relations. The areas of the shaded and solid block for each group are proportional to its dry-weight biomass and protein content in a square meter of test area (key at lower left). Arrows show major food pathways. Dotted lines indicate estimated quantities. For the encrusting algae and protistan film, a greatly magnified view is shown.

Source: Glynn, 1966.

somewhat similar to that of the rocks to which they are fastened, that is, they form a refuge. They are used to little extent by the animals as food, and, though I am well aware that their distribution often coincides with that of some of the so-called dominant or predominant animals of the rocky region, on the whole they exert little influence other than that of protection.

Stephenson and Stephenson (1972) illustrated the importance of considering intertidal plants and animals together.

> Let us suppose that we wish to study the occurrence of the fucoid algae on the British coasts. This can hardly be done effectively unless we realise that the distribution of these seaweeds depends not only on the plants themselves, and on the climatic conditions in which they live, but also upon animals. An area of rock can be free from fucoids simply because limpets, in the course of their browsing, have removed the spores or sporelings--that is, a plant can be absent from an area it might otherwise have colonised, because of an animal.
>
> A second example may be taken from South Africa. There are species of *Gelidium* in that country that, if left to themselves, form short bushes of erect branches a few inches high. But very often an area of *Gelidium* forms the feeding-ground for a limpet, which browses over it so continually that, although the alga does not disappear, it is able to produce nothing more than small flat fronds growing horizontally over the rock, and these make a thin layer only a few millimetres thick. The shape of these prostrate fronds is so unlike that of the normal erect ones that it was not possible to identify them until they had been allowed to grow up into a more normal form by removing the limpets. Here we have an example of the production, by an animal, of a completely different growth form in a plant.
>
> My last example will be taken from the Bermuda Islands. Here, the whole appearance of the tidal belt on the shore can be changed by the activities of animals directed against plants. Some of these animals, such as parrotfish and crabs, peck at the algae growing on the rock, or nip at them with their claws. Other animals, such as snails, limpets, or chitons, rasp the algae from the rock by means of their filelike radulae. These depredations have more than one effect. The rock of Bermuda consists of an aeolian limestone, which weathers into the most intricate surface forms. It is spiky, with innumerable points and sharp edges, hollows, crevices, and cavities, sometimes almost fretted like lace. The scraping activities of the animals mentioned tend to smooth off many of these surface irregularities, so that between tidemarks, the rock becomes increasingly smooth as one goes from higher to lower levels. Here we have a case where the rock itself is affected, as well as the

covering of algae, which becomes a short turf. But here and there another similar effect is visible in Bermuda. We shall see from the later parts of this book that one of the most widespread features of seashores is the existence near high-water level of a horizontal strip in which the surface of the rock is discoloured to a grey or blackish tint by a filmlike incrustation of myxophycean algae or of marine lichens. There are places in Bermuda where one is surprised to find, at the right level, a strip of rock *paler* in colour than the rest, rather than darker. This appears mysterious until it is discovered that the blackish film has indeed developed in such places, as usual, but that the bulk of it has been browsed away, on an unusually comprehensive scale, by littorinid snails. Such examples as these, which could be multiplied, seem to demonstrate the futility of attempting to understand any intertidal population of plants and animals unless both are considered together.

Much has been made of the vertical zonation into separate communities or assemblages within the same intertidal location. These assemblages typically consist of organisms which can withstand prolonged periods of exposure, or assemblages dependent upon a large sessile dominant for protection.

The "widespread features" of intertidal areas discovered by Stephenson and Stephenson (1972) is cited below:

1) Near high-water level is an arid zone subject to conditions transitional between those of land and sea. It is affected by spray, but wetted by waves only in heavy weather or at the higher spring tides, when at least its lower parts become washed or submerged. The number of species inhabiting the zone is relatively small, and includes snails adapted to arid conditions and belonging to the genus *Littorina* and to related genera, or to genera of snails containing similarly adapted species.

2) The surface of the rock in the zone just described, or in its lower part, is commonly blackened by encrusting myxophyceans, or lichens of the *Verrucaria* type, or both. The blackening may exist either as separate patches or as a continuous belt, often overlapping into the zone below; but this "black zone" is one of the most persistent features of shores.

3) The middle part of the shore is the most fully intertidal region and part of it at least is covered and uncovered by the sea every day. The number of species inhabiting the zone is greater than in the drier one above, and typically includes numerous balanoid (acorn) barnacles belonging to such genera as *Balanus*, *Chthamalus* and *Tetraclita*. The upper limit of the zone is marked by the disappearance of barnacles in quantity. There is a strong tendency for the zone to become differentiated into subzones, commonly two or three in number. In the upper of these the barnacles tend to be maximal in quantity and are either the dominant forms or among these. In the lower, they

are usually in competition with other sedentary forms, which may overshadow or obliterate them, though this by no means always happens.

4) The lowest part of the shore is uncovered at spring tides and not at neap tides, and in some places, where wave action is persistently strong, only at the lowest spring tides in calm weather. It supports the fringe of the infralittoral population (that is, the population of the region below tidemarks that is never uncovered), is exposed to the air for a relatively small proportion of the time, and in many places rarely if ever dries off. The population is extremely variable, but is usually rich. In many cold-temperate regions, it consists of a forest of large brown algae (laminarians, for example) with animals and an undergrowth of smaller plants among their holdfasts. On coral reefs, it commonly contains the upper edge of the rich growth of corals that extends down the reef face below low-water level. In warm-temperate regions, it may support (a) a dense covering of simple ascidians (*Pyura*, for example); (b) a dense growth of rather small mixed algae, primarily rhodophyceans; or (c) other communities. Large brown algae may or may not occur here, but if they do, they tend to be less strongly developed than in cold-temperate regions.

5) In the wet zone just described, the encrusting, nonjointed calcareous algae of the family Corallinaceae (referred to broadly as "lithothammia") tend to encrust all surfaces suitable to them, often forming continuous pinkish sheets. This encrustation not only continues below tidemarks, but may also extend above the zone described in paragraph 4. But it does not usually form a continuous growth above the lowest strip of the barnacle zone of paragraph 3, except in pools, caves or other specially damp places.

We may summarize the foregoing paragraphs by saying that seashores show a widespread tendency to develop three principal zones, a *Littorina* zone above, a barnacle zone in the middle, and a wetter zone of variable population below. In addition, there is typically a blackish myxophycean or lichen zone at a high level, and an incrustation of lithothamnia over all the lower parts of the rock. Perhaps it should be added that, above the *Littorina* zone, there are often other zones distinguished by coloured lichens (orange, grey, green, white, brown) belonging to species other than those characteristic of the black zone. But as these higher zones belong to the maritime land flora rather than to the tidal zone, we shall be little concerned with them here.

Areas having rocky shores or rocky outcrops on otherwise sandy beaches have a larger and more diverse intertidal community than sandy beaches. The total area comprising the rocky intertidal habitat varies seasonally on the Pacific coast. The heavy surf during the winter greatly increases the amount of rocky shores as it washes much of the sand away from the beaches.

The movement of sand is important to the state of the rocky intertidal community. This movement can smother existing intertidal organisms, interfere with spawning and larval activities in addition to changing the amount of rocky shore available to the intertidal community.

The relative duration and periods of tidal exposure is another important aspect of the rocky shore intertidal community. Because of the degree of tidal exposure, the community changes over a vertical distance of only several feet. Rocky shore intertidal communities are distinguished and classified by their vertical zonation. The following, coming from Ricketts, Calvin, and Hedgpeth (1968), was primarily based upon the animal component of the community.

Another important ecological factor on a rocky shore intertidal community is the degree of wave shock. With increased wave force, the difficulty of an organism to hold on to the substrate or otherwise maintain its position increases.

The degree of wave shock can modify the vertical zonation pattern of a semi-protected area and alter the species composition of the community. Ricketts, et al., (1968) concluded that a vertical zonation of the rocky intertidal community into four units was the most practical. Their classification shown in Table III.C-1 is summarized as follows:

Zone 1 Splash zone (supralittoral or littorina zone) (1.5 m {5 feet} above low mean tide)

Zone 2 High tide on upper horizon (1.5 to 0.75 m {5 feet to 2.5 feet} above lowmean tide)

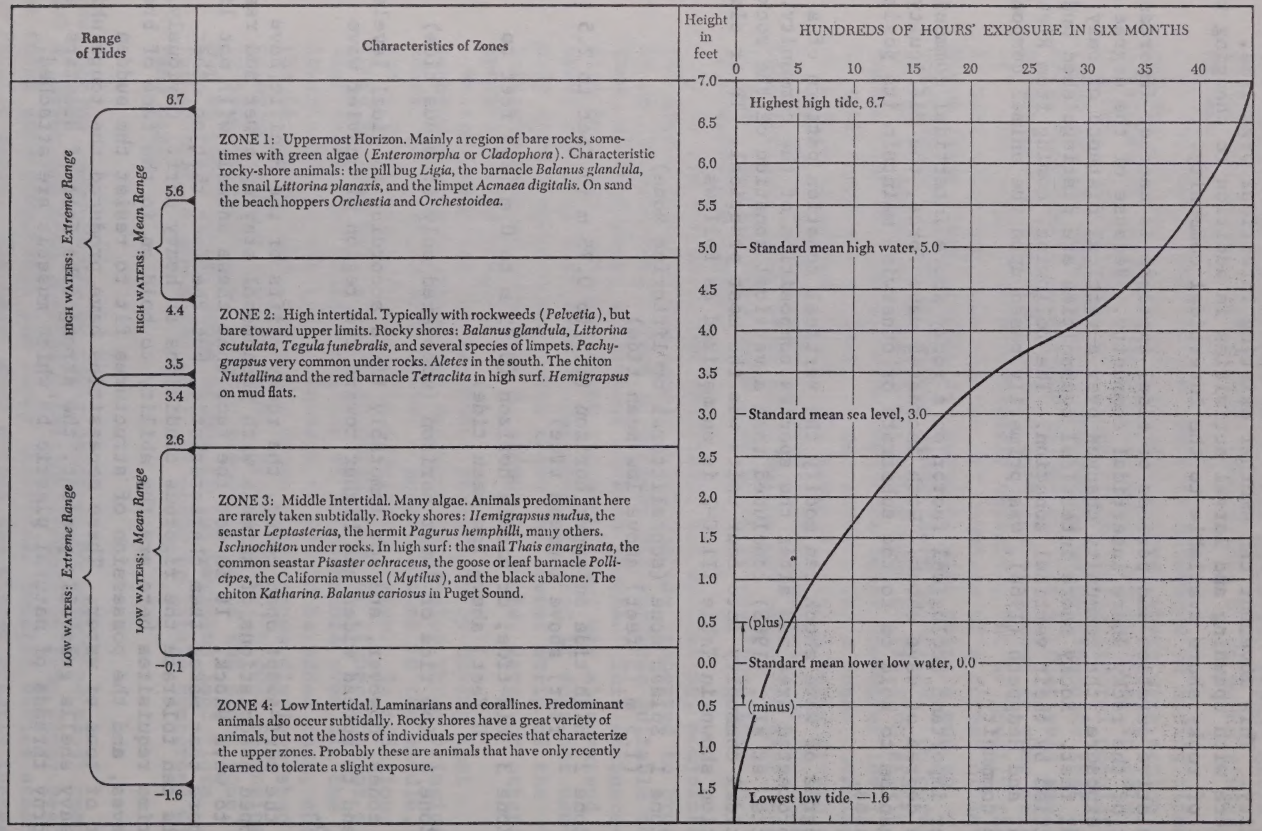
Zone 3 Mid-tide, or middle horizon (0.75 m to 0 m {2.5 feet to 0 feet} above low mean tide)

Zone 4 Low tide or lower horizon (uncovered only at minus tide)

These zones, however, are not immutably fixed according to tidal levels, but tend to spread wider and higher toward the region of heavier wave action.

Along the surf-swept open coast, the rocky cliffs of the Pacific have developed associations of animals with phenomenal staying power and resistance to wave shock. It is not the fact that these animals will not live elsewhere that makes them characteristic, but the fact that no other animals can tolerate the rigorous conditions of heavy surf. Obviously, the prime requisites here are the ability to hold on in the face of breaking waves, and the possession of structures fit to resist the sudden impact of tons of water. These necessities have produced the tough skins and heavy shells generally present, the strong tube feet of seastars, and the horny threads of natural plastic by which mussels are attached.

Table III.C-1


Range of Tides
Characteristics of Zones
Height in feet
HUNDREDS OF HOURS' EXPOSURE IN SIX MONTHS
0 5 10 15 20 25 30 35 40
HIGH WATERS: Extreme Range
HIGH WATERS: Mean Range
LOW WATERS: Mean Range
LOW WATERS: Extreme Range
6.7
5.6
4.4
3.5
3.4
2.6
−0.1
−1.6
ZONE 1: Uppermost Horizon. Mainly a region of bare rocks, sometimes with green algae (Enteromorpha or Cladophora). Characteristic rocky-shore animals: the pill bug Ligia, the barnacle Balanus glandula, the snail Littorina planaxis, and the limpet Acmaea digitalis. On sand the beach hoppers Orchestia and Orchestoidea.
ZONE 2: High intertidal. Typically with rockweeds (Pelvetia), but bare toward upper limits. Rocky shores: Balanus glandula, Littorina scutulata, Tegula funebralis, and several species of limpets. Pachygrapsus very common under rocks. Aletes in the south. The chiton Nuttallina and the red barnacle Tetraclita in high surf. Hemigrapsus on mud flats.
ZONE 3: Middle Intertidal. Many algae. Animals predominant here are rarely taken subtidally. Rocky shores: Hemigrapsus nudus, the seastar Leptasterias, the hermit Pagurus hemphilli, many others. Ischnochiton under rocks. In high surf: the snail Thais emarginata, the common seastar Pisaster ochraceus, the goose or leaf barnacle Pollicipes, the California mussel (Mytilus), and the black abalone. The chiton Katharina. Balanus cariosus in Puget Sound.
ZONE 4: Low Intertidal. Laminarians and corallines. Predominant animals also occur subtidally. Rocky shores have a great variety of animals, but not the hosts of individuals per species that characterize the upper zones. Probably these are animals that have only recently learned to tolerate a slight exposure.
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.5
1.0
1.5
Highest high tide, 6.7
Standard mean high water, 5.0
Standard mean sea level, 3.0
(plus)
Standard mean lower low water, 0.0
(minus)
Lowest low tide, −1.6

Vertical zoning of animals on the Pacific coast

Source: Ricketts, et al., 1968.

The force of the waves on stretches of completely open coast is so great that animals up near the high-tide line are wetted by spray on all but the lowest tides. Consequently, there is not the relatively sharp zonation that we find elsewhere, and some of the most obvious animals are fairly well distributed throughout the intertidal zone.

Ricketts and Calvin described the various vertical zones and habitats within them (Figure III.C-9). These descriptions are applied to rocky shores in general.

(1) Spray zone - This is a bare rock area in the main, but sometimes there are sparse growths of green algae. It is inhabited by hardy, semiterrestrial animals.

(2) High tide zone - In this belt there is a greater variety of species and a tremendously greater number of individuals of many of the species represented than in the highest zone. Here there are some more or less permanent tide pools, with their active fauna of hermit crabs, snails, and crabs. Barnacles occur here also, certainly larger and possibly in greater abundance. Plants begin to appear in the uppermost part of this zone, and grow lush in its lower part. These plants not only provide bases of attachment for sessile animals, but furnish shelter for others that adhere to the rock, and protect them from desiccation.

(3) Mid-tide zone - This area, zone 3, is below mean sea level, and is largely covered by most high tides. The higher zones seem relatively barren by comparison with the teeming life of this mid-region, which is exceeded in density only by that of the outer tidelands. Here plants grow in great profusion. These plants, in providing protection from deadly sunlight and drying, are of importance to the animals, which are predominantly intertidal forms and rarely occur in deep water.

The variety of animals associated in this zone is so great that it seems desirable to consider them according to a further division of habitat, as follows: exposed rock; protected rock; underrock; burrowing; pool; root and holdfast.

Exposed Rock Habitat. These are animals living on the tops and sides of rocks and ledges, exposed to waves, sun, and wind.

Protected Rock Habitat. Animals here are attached to, or living on, protected rocks and rockweed.

Many of the commonest inhabitants of this subregion can scarcely be considered obvious, since in order to see them advantageously one must almost lie down in the pools, looking up into the crevices and under ledges.

Under-Rock Habitat. These are animals found on the underside of loosely embedded rocks (but not in the substratum) or between adjacent rocks and boulders where there is no accumulation of substratum. This area offers the maximum of protection from wave shock, sunlight, and desiccation.

Burrowing Habitat. Animals of the burrowing habitat occur in the mud, sand, or gravel substratem underlying tide-pool rocks. A small stout trowel is a good tool here, for the surface boulders are often resting on a matrix of muddy gravel bound together by chunks of rock of varying sizes. The normal expectancy would be that the sand or mud under rocks would harbor forms similar to those burrowing in the sand or mud of estuaries. This proves true to some extent, although the under-rock substratum animals actually seem to form a fairly specific assemblage.

Tide pools are small depressions filled with water, even during low tide. Water temperatures reach extreme highs during the summer, and salinities can fluctuate greatly during rainfall or high air temperatures.

(4) Low tide zone - Many of the middle-horizon animals occur here also, but much of the population consists of animals unable to exist higher up and not so accustomed to the rhythm of the tides. This trememdously crowded environment contributes a greater number of species than all the other tidal levels. Not only do the waters teem, but there is no rock too small to harbor some living thing, and no single cluster of algae without its inhabitants. Since these creatures live and thrive in an environment that seems utterly strange to us, it is no wonder that we find interest in their ways of feeding, of breathing, of holding on, of ensuring the continuity of their kind, or in their strangely different weapons and methods of attack and escape.

In this zone, very few animals are exposed to wave action, sun, and wind on unprotected rock faces, except on open coasts where the surf is high.

The habitats of rock, under rock, burrowing, etc. are also present at the low tide zone.

Succession. The question of whether repopulation of a rocky shore intertidal area precedes in a true ecological succession as on many terrestrial habitats remains unanswered. According to ecological theory, and demonstrated at several forest types during true ecological succession, the first group of organisms to settle prepares the way for the next by modifying the substrate, providing suitable or in some way modifying the environment. This succession is a definite sequence to the climax stage or most stable condition; thus, conditions leading to change are generated within the community by members of the community. The opposing viewpoint maintains there is no necessary sequential series nor is it necessary for earlier settlers to modify the environment for the climax community.

Organisms settle at approximately the same place on top of whatever has settled before, and the most vigorous organisms will crowd out the earlier arrivals.

Evidence for true ecological succession was presented by Hewatt (1935). Contrary to what might be expected at first guess, the mussel bed does not start with young mussels settling on a bare rock. Hewatt, as part of his work at Pacific Grove, scraped a square yard of mussel bed bare in November, counting the animals he removed, and made subsequent counts every few months for a year. His results are best summarized in Table III.C-2.

Table III.C-2

REESTABLISHMENT OF A MUSSEL BED

	1931	1932						
	Nov. 23	Feb. 19	Mar. 4	Apr. 25	June 3	July 18	Oct. 13	Dec. 26
Algae		xxx						
Acmaea spp.	319	61	232	314	353	331	997	792
Amphissa versicolor	39							
Balanus glandula	872		95	2126	1967	1904	2175	2374
Cirolana harfordi	926							
Leptasterias aequalis	6							
Lottia gigantea	10	1	7	8	11	11	15	15
Mytilus californica	1612			55	51	7	53	89
Nuttallina californica					2	34	14	9
Pachygrapsus crassipes	14							
Petrolisthes cinctipes	416							
Phascolosoma agassizi	327							
Pollicipes polymerus	356		76	109	109	109	109	108
Tegula brunnea	17							
Tetraclita squamosa	78		423	416	378	371	359	329
Thais emarginata	218			2	7	367[a]	47	59

Source: Hewatt (1936).

aAverage size, 5 mm (0.2 inches).

As can be seen, the first event was the growth of a film of algae, accompanied by a vanguard of limpets grazing on it. Then came the barnacles. At the end of the observation period, the barnacles were still in the majority, and none of the shelter required by the crevice-loving animals was yet available. Unfortunately, Hewatt was unable to follow this through until the test square had returned to "normal."

The subtidal studies by Haderlie (1974) in Monterey Harbor have all suggested true succession in shallow waters. No matter what time of year the settlement was allowed to commence, the sequence was essentially the same.

First, a bacteria-diatom film appeared; these were followed, in sequence, by bryzoans, ascidians, and mussels.

Shelford (1930) represented the opposite viewpoint and stated "there is development but probably little or no succession in the growth of the intertidal communities on rock." In support of Shelford's theory, alternative mechanisms have been proposed to explain the appearance of stages in the redevelopment of rocky intertidal zones. Kitching (1937), Bokenham (1938), and Northcraft (1948) discussed recolonization of intertidal algae in terms of differential rates of growth. Rees (1940) suggested that species comprising early stages of redevelopment were in the plankton as larvae during much of the year and were able to settle as soon as new or denuded substrates were available for colonization. Connell (1972) recently proposed the reasons for the orderly sequence of recolonization in the rocky intertidal are the differences in the length of breeding seasons, motility of planktonic stages, rates of growth after settlement, and ultimate size reached by species, rather than successive modifications of the environment by the organisms themselves.

Working in northern California, Cimberg (1975) reported the appearance with time of recolonizing species, serving stages in the redevelopment of each zone, was a function of the time of settlement, speed of growth, and the ability to compete for space. Since environmental modifications by earlier stages did not appear to be necessary for the appearance of later forms in this study or in similar investigations, succession as defined by Odum and Shelford has not been demonstrated to occur in the rocky intertidal; instead, there is "sequential non-successional redevelopment."

Perhaps more important from a practical standpoint than the method of succession is the time required for recovery or reestablishment to occur. There are essentially three phases in reestablishment of an area: (1) when members of the original species assemblage settle; (2) when the members of the original species assemblage reach reproductive maturity, spawn and therefore propetuate the population (biological recovery); and (3) when the stature of the population, with respect to species composition, percent cover, size or age of individuals, reach pre-destruction or "normal" conditions. The time required to complete each stage will obviously require far greater time.

The time required for reestablishment of the normal population structure in mussel beds is relatively long. Hewatt (1935) reported that after 2.5 years the denuded mussel bed had not returned to normal. MacGinitie (1939) pointed out that Hewatt cleared an area at the upper portion of the mussel zone rather than in its center, and it is not known if recovery would have proceeded more rapidly here. Chan and Molina (1969) reported it took ten years for a cleared strip of mussels to return to predestruction population structure. Ricketts, et al., (1968) reported other studies on denuded surfaces suggest that it may take five years for a mussel bed to become established.

Stephenson and Stephenson (1972) analyzed data by Keen (1937) (Figure III.C-13) and their own (Figure III.C-12). Their views are summarized below:

> A particular feature of the west coast is the relatively high proportion of species with a long range from north to south, and vice versa (Figures III.C-10 and 11, categories 1 and 6).
>
> The Southern Group (Categories 2-5). This is the most distinctive group. The areas showing the most definite change from southern to central species are those around Pacific Grove and Point Conception (Figure III.C-12). There is, undoubtedly, a southern biota south of Point Conception that includes warm-temperate forms that die out in Lower California or in the Gulf of California. The tropical fauna en masse does not reach the United States. Some southern species have a long northern extension beyond Point Conception, and have a marked influence on the composition of the central group.
>
> An examination of the known southern limits of this southern group reveals that about three-quarters of the species that belong to categories 2, 3, 4, and 5 have their southern limits in Lower California or in the Gulf of California. Some may overlap into tropical regions, but they are only outliers of the main populations. Only about one-quarter seem to be genuine tropical species that extend north. This is probably significant, although the region needs more exploration. La Jolla is not really tropical, as it lacks any great number of stenothermic tropical forms; it can only be regarded as a warm-temperate area.
>
> The Northern Group (Categories 7-10). This is not as clear-cut as the corresponding group on the Atlantic coast, but it certainly exists. It includes many species with long southern extensions that affect the populations of the central regions. There is no place at which northern forms are delimited as markedly as the southern ones are at Point Conception (Figure III.C-13).
>
> The Central Group (Categories 11-15). Many of the species of this group extend a very long distance--southwards to San Diego and northwards to Vancouver Island. Its greatest number of species are on the coast between San Francisco and San Diego.
>
> From the data given above, it is clear that a warm-temperate biota is the dominant one on the west coast. From our own work and from other records of the ranges of species it seems that there is a definite central group of species with its extreme limits at San Diego and Vancouver. At Pacific Grove,

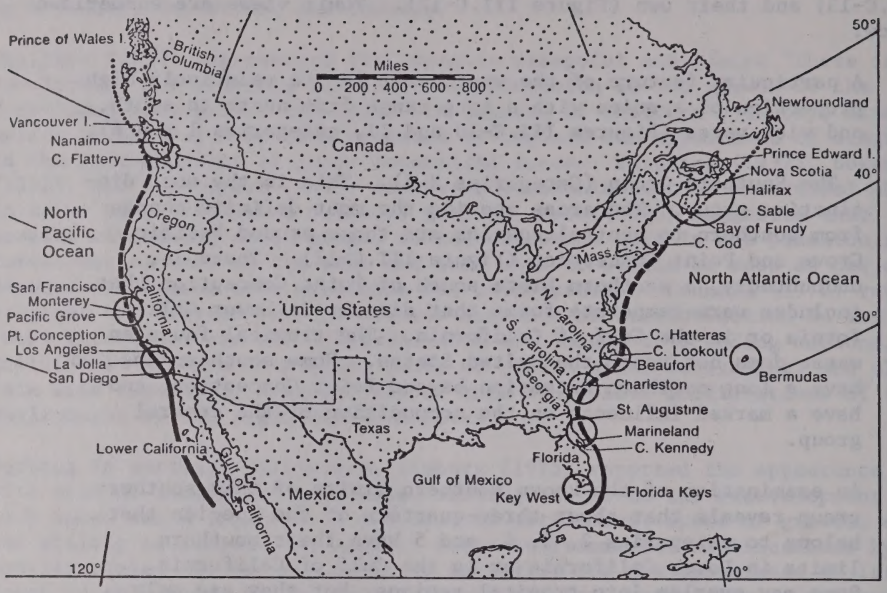


FIGURE III.C-10

A map of North America showing the locations of places named in the text. Circles indicate the areas studied. The thick lines along the east and west coasts illustrate the extent of the three main groups of species: *unbroken lines,* the southern groups; *broken lines,* the central groups; *dotted lines,* the northern groups.

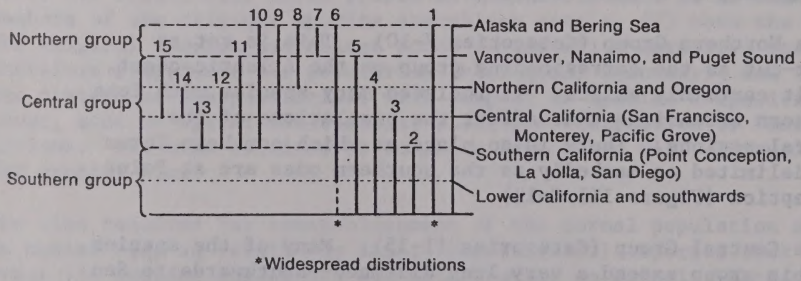


FIGURE III.C-11

The various categories into which the three main groups of west-coast species may be subdivided according to the occurrence of the species along the coast between specified stations. The number of categories included in each group is partly dependent on the number of species studied. On the right-hand side are given the names of the stations, and on the left, braces indicate the stations defining the geographical limits of each group. An analysis of this figure is given in the text.

Source: Stephenson and Stephenson, 1975.

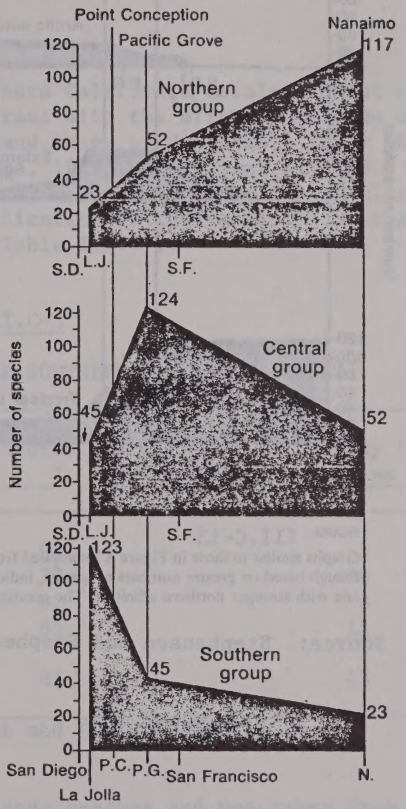


FIGURE III.C-12

The distribution of the three main groups of the biota of the west coast of North America. The graphs are based on data collected by the authors, and refer mainly to the commonest species. The graph for the northern group shows that of the 117 species collected at Nanaimo, 52 extended to Pacific Grove and 23 to La Jolla; the other graphs can be similarly interpreted.

Source: Stephenson and Stephenson, 1975.

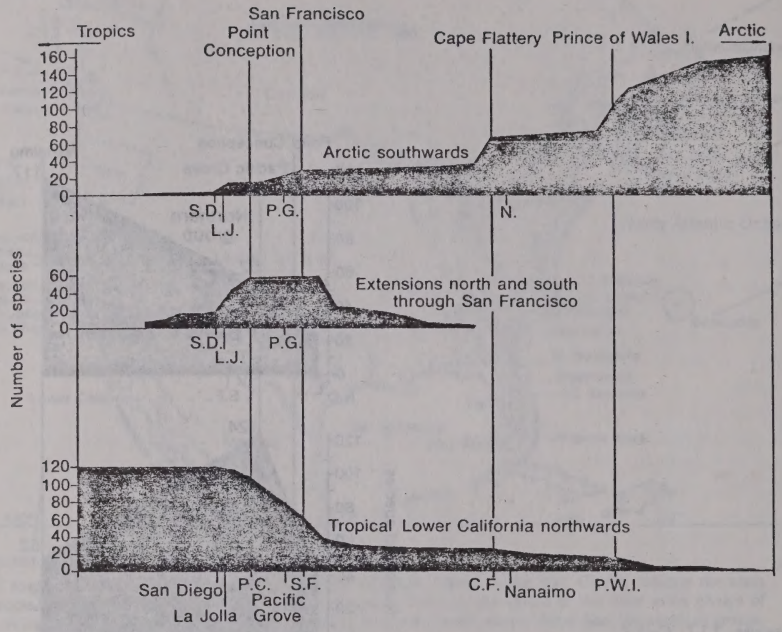


FIGURE III.C-13

Graphs similar to those in Figure 3.7 compiled from data taken from Keen (1937). These graphs, though based on greater numbers of species, indicate the same three main groupings, the central one with stronger northern affinities. The greater number of species smooths out the lines.

Source: Stephenson and Stephenson, 1975.

only 1 percent of true southern species extend into this extensive central group, but 13 percent of northern species do so, which indicates that the central group has more affinity with the north than with the south.

Naturally, further work may show that there are more than three main groups, but it must be remembered that our classification was founded, on the whole, on the commonest animals.

Approximately 20 percent of the Southern California mainland coast has sandy beaches. This is in sharp contrast with the offshore islands which, with the exception of San Nicolas Island, have predominately rocky shores (California Department of Fish and Game, 1973). Approximately 133.6 km (83.5 miles) (76 percent) of Santa Barbara County's shoreline is classed as sandy beach. The shoreline classification of the remaining Southern California counties are tabulated in Table III.C-3.

Table III.C-3

SHORELINE CLASSIFICATION OF THE SOUTHERN CALIFORNIA BIGHT

County	Rocky Shores Miles	%	Sandy Beaches Miles	%
Ventura	38	93	3	7
Los Angeles	51	77	26	24
Orange	38	92	3	8
San Diego	65	85	11	15
Total	192	81	43	19

Source: California Department of Fish and Game (1973).

Visual No. 2 shows the locations of sandy beaches and was taken from Corps of Engineers and Dames and Moore (1971).

Littler, et al., (1977) reported on the first year study of the BLM sponsored study at 6 islands and 4 mainland rocky intertidal sites (Figure III.C-14). The following with very few changes was taken from Littler (1977).

No comparable spectrum of rocky intertidal systems has been examined with the level of sampling effort and resolution of data provided herein. The scope of this work is such that temporal and spatial variations of the macroinvertebrate and macrophyte species have been assessed in terms of

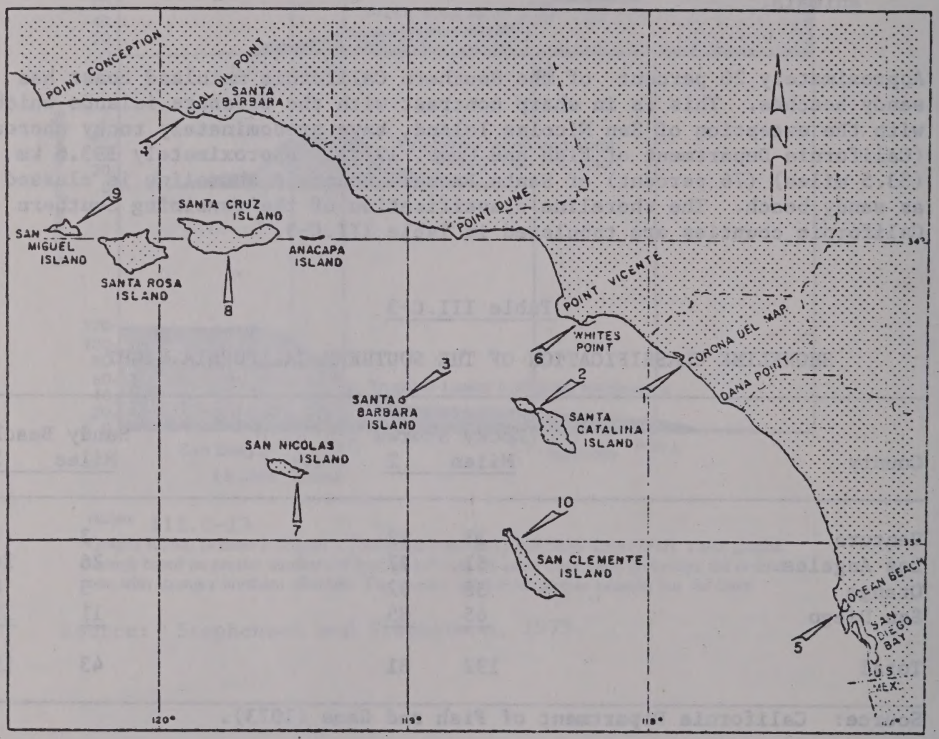


Figure III.C-14 Location of Rocky Intertidal Study Sites.

Source: Littler (1977).

tidal location, cover, frequency, density, wet weight, dry weight, ash-free dry weight, species diversity, evenness, richness, community stratification, cluster analysis, and discriminant analysis. These descriptive parameters were used at each of 10 markedly different sites during 4 separate quarters of the year to characterize a range of intertidal systems and to relate important features of distribution and abundance to possible causal (biotic and abiotic) features of the environment. The complexity of characterizations and comparisons of the rocky intertidal communities is reflected in the diversity of macrobiotic constituents in the Southern California Bight; Table III.C-4 provides an abbreviated listing by major taxonomic groups of macrophytes and macroinvertebrates collected at the study sites during the past year.

Table III.C-4

NUMBERS OF TAXA BY MAJOR TAXONOMIC GROUPS
COLLECTED DURING THE YEAR AT ALL TEN SITES

Major Groups		Number of Taxa Collected
Macrophytes		
Bacillariophyta		1
Chlorophyta		27
Cyanophyta		4
Phaeophyta		34
Rhodophyta		152
Spermatophyta		2
Total		220
Macroinvertebrates		
Annelida	- Polychaeta	12
Arthropoda	- Crustacea	27
Cnidaria	- Anthozoa	6
Cnidaria	- Hydrozoa	10
Chordata	- Ascidiacea	4
Echinodermata	- Asteroidea	8
Echinodermata	- Echinoidea	2
Echinodermata	- Holothuroidea	2
Ectoprocta (Bryozoa)		8
Mollusca	- Bivalvia	15
Mollusca	- Cephalopoda	1
Mollusca	- Gastropoda	97
Mollusca	- Polyplacophora	12
Platyhelminthes	- Turbellaria	3
Porifera	- Calcarea	2
Porifera	- Demospongiae	18
Total		227

Source: Littler (1977).

A total of 447 taxa was recorded during the year from all 10 study areas. The number of macrophyte taxa (220) was about equal to the number of macroinvertebrate taxa (227). Over half of the macrophytes recorded were Rhodophyta, but Phaeophyta (especially *Egregia menziesii*) was the major contributor of biomass. Of the macroinvertebrates, gastopods contained by far the most taxa (97).

Biological cover in the rocky intertidal is of primary ecological significance because space (and light) are often limiting resources (see Connell, 1972). Major macrophytic cover throughout the 10 Southern California Bight stations was contributed predominantly by the blue-green algae (overall mean of 20%), the red algae *Corallina* spp. (9%), the red alga *Gigartina canaliculata* (8%), the brown alga *Egregia menziesii* (6%), and two trachaeophytes *Phyllospadix* spp. (4%). Most of these were important at many of the sites, except for *Phyllospadix* spp. which was abundant only at Coal Oil Point and San Nicolas Island (the two sites most affected by sand), while blue-green algae were important at all sites except these two sites. In terms of cover, the dominant macroinvertebrates were the anemone *Anthopleura elegantissima* (3% overall cover), the mussel *Mytilus californianus* (2%), and the barnacles *Chthamalus fissus/dalli* (2%). These four were present at all 10 sites; however, *A. elegantissima* was predominant only at Coal Oil Point and San Nicolas Island.

Organic dry weight is also an ecologically significant parameter because it represents the standing stock of organically bound energy available to higher trophic levels. As indicated by Glynn (1966) most of this source is not utilized directly, but becomes more important as a food source for the community when it has undergone various stages of decomposition and decay.

Egregia menziesii was by far the predomonant organism with an overall mean of 155 g/m^2 followed by the brown algae *Pelvetia fastigiata* (70 g/m^2), *Phyllospadix* spp. (70 g/m^2), the brown algae *Eisenia arborea* (57 g/m^2), *Gigartina canaliculata* (56 g/m^2), the brown algae *Halidrys dioica* (48 g/m^2), and *Corallina* spp. (29 g/m^2). All of these exhibited widespread importance except *Phyllospadix* spp. (abundant at four sites), *Pelvetia fastigiata* (predominant only at three sites), and *Eisenia arborea* (dominant only at Santa Catalina Island). Macroinvertebrate biomass throughout the 10 sites resided mainly in *Anthopleura elegantissima* (33 g dry organic weight/m^2), *Mytilus californianus* (22 g/m^2), the purple urchin *Strongylocentrotus purpuratus* (9 g/m^2), and the barnacles *Tetraclita squamosa rubescents* (4 g/m^2), and *Chthamalus fissus/dalli* (2 g/m^2). All of these exhibited widespread abundance except *T. squamosa rubescens*, which was an important contributor of biomass at only four of the sites; most of the *A. elegantissima* biomass occurred at Coal Oil Point while Santa Cruz Island and Corona del Mar contained most of the *S. purpuratus* biomass.

On all sites having a continuous rocky slope, Littler was able to clearly recognize the three nearly "universal vertical zones" described by Stephenson and Stephenson (1972).

They were further able to differentiate from 3-7 subzones and 6-11 subassemblages within the 3 generalized zones by statistical cluster analysis.

Sites having the greatest number of seasonally constant species assemblages or subassemblages (revealed by the cluster analysis) were San Miguel Island with 11, Santa Catalina Island with 10, and Ocean Beach with 10. Corona del Mar and San Nicolas Island had only six assemblages. The greatest zonational complexity was observed at Santa Cruz Island (7 zones), Santa Barbara Island (7 zones), San Miguel Island (6 zones), and Santa Catalina Island (6 zones). Greater zonational complexity occurred over relatively even flows of very rough-textured volcanic rock. The least zonation was evident at Corona del Mar (2 zones), Coal Oil Point (3 zones), Whites Point (4 zones), and San Clemente Island (4 zones). Reductions in zonal patterns appear to be related to lack of a high intertidal zone, mosaic habitat patterns, instability of boulder substrates, and environmental stresses such as sand inundation.

Seasonal means averaged for all 10 sites indicated a general lack of any widespread or consistent patterns or tendencies, except for a very slight lowering of most parameters following the winter months. This strongly suggests that local or even site-specific conditions tend to predominate most often and obscure the broad climatic effects. Climatic conditions appeared to influence the subtler but more widespread populational changes manifested by such macrophytes as *Egregia menziesii*, *Laurencia pacifica*, *Sargassum agardhianum*, and *Gigartina canaliculata*. Barnacles and most other macroinvertebrates recruited strongly during the winter-spring period, while the sea hare *Aplysia californica* was observed producing abundant egg masses in late July at Corona del Mar. Numerous workers (see Emery, 1960; Schwartzlose, 1963; Jones, 1971) have pointed out that the Southern California Bight is a very unusual region located within the overlapping boundaries of two major biogeographic regions, resulting in a concomitantly complex oceanographic and climatological regime. Throughout the Southern California Bight, there exists a mosaic of frequently changing water temperatures, substrates, upwelling conditions, wave exposures, water transparencies, levels of natural and human-induced disturbances, and nutrient concentrations. Therefore, it is not very surprising that intertidal systems should show a high degree of site-specific individuality.

The data appear to suggest a trend in regard to substrate type. For example, those sites (i.e., San Miguel, Santa Cruz, Santa Barbara, and Santa Catalina Islands) having relatively even slopes created by flows of the very rough-textured volcanic rock (which holds small pockets of moisture) have considerably more macroinvertebrate taxa (mean of 80) than the other six sites (mean of 62); San Miguel Island was an exception with only 55. Corona del Mar (71), Whites Point (69), and San Clemente Island (65) were reasonably high in macroinvertebrate taxa, possibly related to the relatively structured nature of the substrate at these sites (i.e., nearby boulder habitats having a broad spectrum of sizes and stability). The three remaining sites which were entirely of smooth sandstone or siltstone contained a mean of only 55 macroinvertebrate taxa. Also, the greatest zonal complexity and constancy was observed for the same four volcanic

island sites (mean of 6.5 zones), followed by siltstone/sandstone habitats (i.e., Corona del Mar and San Clemente Island) with the mean number of zones being only 3.0. Sites shown to be periodically inundated by sand (i.e., Coal Oil Point, San Nicolas Island, Whites Point, and Corona del Mar) had a mean of 3.5 zones. Reduction in zonal pattern appears to be most closely related to a reduction in vertical height of the rocky shoreline above MLLW, the mosaic-like habitat distribution, instability of boulder substrates, and environmental perturbations such as sand inundation. These last two factors were shown to have especially dramatic effects, a point not very well documented in the existing literature on intertidal ecology.

All 10 sites were subjected to statistical cluster analyses based on the combined overall mean abundances of macrophyte and macroinvertebrate populations.

Cluster dendrograms based on frequency (Figure III.C-15) and cover (Figure III.C-16) are most revealing and statistically more reliable because they are based on a greater number of samples (i.e., the photo-samples). Frequency distributions showed groupings between the two warm-water biotas (Santa Catalina and San Clemente Islands), the two biologically intermediate islands (Santa Barbara and Santa Cruz), and the two sites most heavily affected by sand inundation (San Nicolas Island and Coal Oil Point).

Because space and light have been shown (see Connell, 1972) to be limiting resources in the rocky intertidal, cover was felt to be ecologically the most meaningful parameter for comparison between sites. The cover dendrogram (Figure III.C-16) produced groupings that agreed closely with intuitive opinions (based on subjective observation) regarding similarities and dissimilarities between sites. For example, the islands having mixtures of cold water and warm water biotas (Santa Barbara and Santa Cruz) clustered together with the Ocean Beach site which also had large amounts of macroinvertebrate cover. The two leeward warm water sites (Santa Catalina and Miguel and San Nicolas Islands) formed a second cluster group while the oil-polluted site (Coal Oil Point) was not closely correlated with any of the other sites.

It is interesting and quite revealing to compare island with mainland rocky intertidal habitats. First, a direct comparison was made between sites considering only the lower portions of the shoreline. The means for the lowest three 0.3 m (1.0-foot) intervals that could be sampled intertidally throughout the year were determined for each of the 10 sites and are presented in Table III.C-5. The average lower dry organic biomass for islands (1355 g/m^2) was more than double that for mainland sites (620 g/m^2). The bulk of this biomass was contributed by macrophytes (1238 and 527 $gm/^2$ for island and mainland sites, respectively) and mostly resided in the larger brown algae (e.g., *Egregia, Halidrys, Eisenia*) and surf grasses (*Phyllospadix* spp.). The same trend held for comparisons between lower intertidal macrophytic cover (118% island vs. 102% mainland) but the differences were not as pronounced as in the case of biomass. Lower

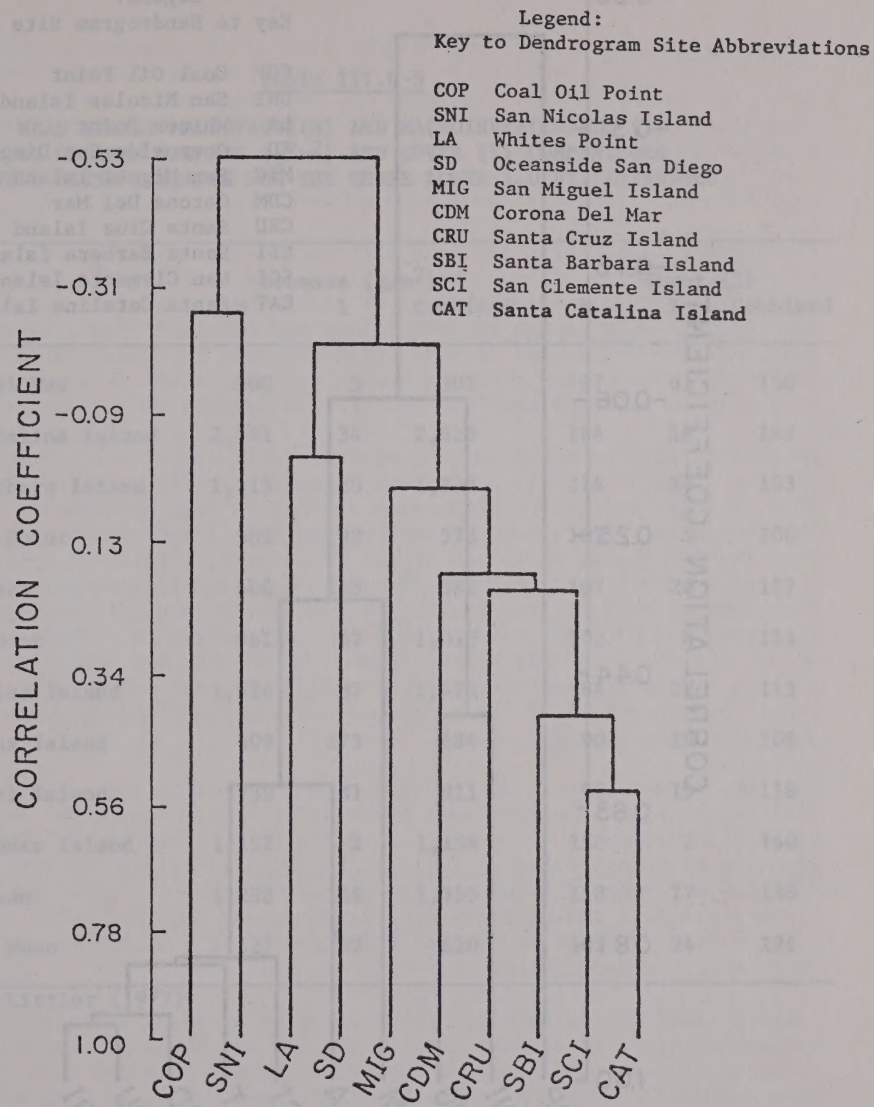


Figure III.C-15 Dendrogram Display of Differential Clustering of All 10 Study Sites Using the Combined Frequency Values.

Source: Littler (1977).

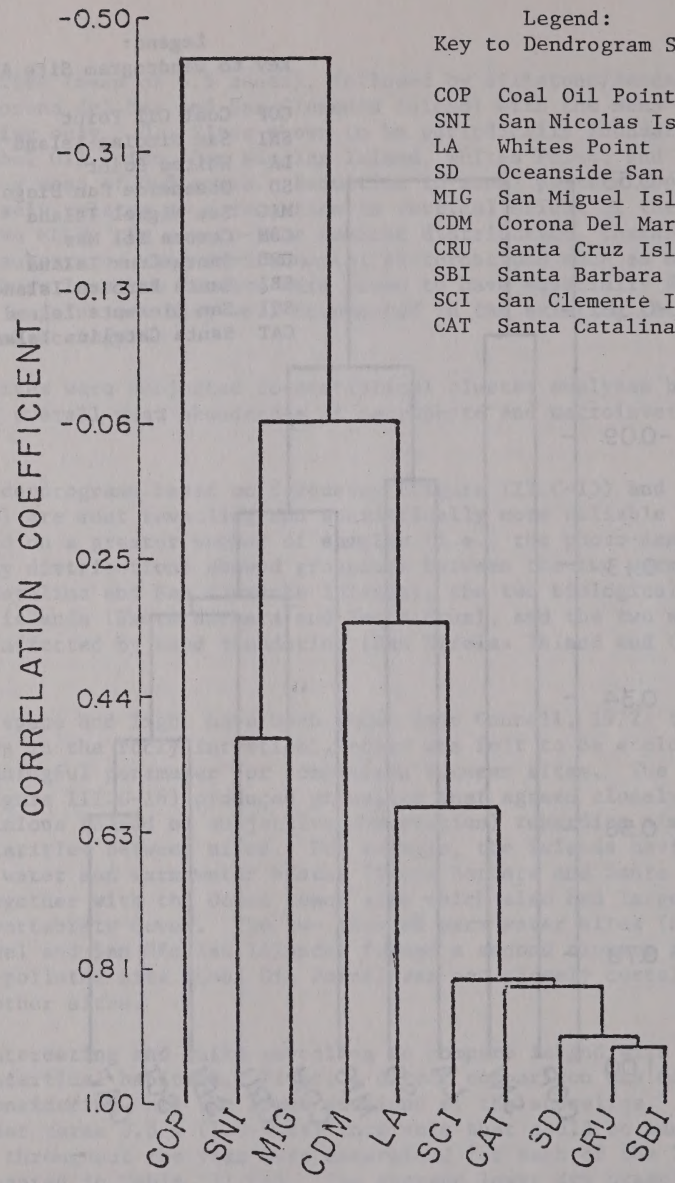


Figure III.C-16 Dendrogram Display of Differenital Clustering of All 10 Study Sites Using the Combined Cover Values.

Source: Littler (1977).

Table III.C-5

MEAN YEARLY MACROPHYTE(M) AND MACROINVERTEBRATE (I) DRY ORGANIC BIOMASS (g/m^2) AND COVER (%) COMPARISONS BETWEEN SITES AVERAGES FOR THE THREE LOWER 1.0 FT. INTERVALS

Sites	Biomass (g/m^2)			Cover (%)		
	M	I	Combined	M	I	Combined
Corona del Mar	300	3	303	97	61	158
Santa Catalina Island	2,591	34	2,625	164	18	182
Santa Barbara Island	1,213	120	1,333	114	19	133
Coal Oil Point	381	192	573	103	5	108
Ocean Beach	466	123	589	107	20	127
Whites Point	961	52	1,013	103	8	111
San Nicolas Island	1,334	87	1,421	86	27	113
Santa Cruz Island	409	275	684	90	19	109
San Miguel Island	730	181	911	99	19	118
San Clemente Island	1,152	2	1,154	158	2	160
Island Mean	1,238	116	1,355	118	17	136
Mainland Mean	527	92	620	102	24	126

Source: Littler (1977).

intertidal island dry organic biomass (116 g/m^2) exceeded mainland values (92 g/m^2) for macroinvertebrates, while the reverse was true for the cover data (17% island macroinvertebrate vs. 24% mainland). This reversal is largely due to inordinately large cover (61%) contributed by *Chthamalus* (a form low in biomass/unit of cover) at the Corona del Mar site -- an unstable boulder habitat having large areas of space continually made available to rapid colonizers such as barnacles.

Even when considering that there were more island sites sampled (6 vs. 4), the higher numbers of taxa that occurred only on islands, particularly of macroinvertebrates, is striking. Of the macrophytes taken in the quadrat samples, 117 were common to both island and mainland sites, 25 were from mainland sites only, and 39 were found uniquely in island samples. For macroinvertebrate taxa, 86 were common to both islands and mainland, 33 were only in mainland samples, and 86 were sampled only from islands.

Relatively more taxa (45 to 140) were uniquely sampled at three or less sites (Figure III.C-17), while many fewer (15 to 28) were found at more than 5 sites, and this relationship applied to both macrophytes and macroinvertebrates. There were 15 macrophytes and 13 macroinvertebrates that occurred in samples at all 10 of the study areas (Table III.C-6), while another somewhat smaller group (6 macrophytes and 12 macroinvertebrates) were sampled at 9 of the 10 sites. It is quite revealing on this last note that the site where most (66%) of these otherwise ubiquitous macrophytes did not occur was Whites Point. There were two other sites where certain widespread macroinvertebrates also were not sampled; Coal Oil Point where one half of these dropped out and San Clemente Island where one third were uniquely absent.

Coal Oil Point samples, on the other hand, contained the largest number of macrophyte taxa (19) found only at one site, while Corona del Mar and San Nicolas Island had the fewest (2). Santa Cruz Island had far more site specific macroinvertebrates (27) and San Nicolas Island (3) has the least, followed by Coal Oil Point and San Miguel Island (4). This led Littler to hypothesize that the presence of oil may act at Coal Oil Point to eliminate certain widespread species while providing a unique habitat for other more uncommon forms.

Samples could not be obtained from the upper vertical zones at one of the six island sites (i.e., San Nicolas Island) and three of the four mainland sites (i.e., Coal Oil Point, Whites Point, and Corona del Mar) because of sand inundation. On the assumption that these sites, as well as the six others, are reasonably representative of their respective habitats (inland shorelines are much less subject to sand and gravel inundation than mainland shorelines), Littler felt that cautious comparisons of tendencies (e.g., between mainland and island sites) would be instructive. Subsequent studies sponsored by BLM may determine if this is true, at least for the islands. In other words, it was essential that mainland rocky intertidal systems which often had their upper shorelines inundated by sand and gravel, and were thereby poor in upper intertidal fauna, be documented. Similarly, it was just as essential to represent the island intertidal

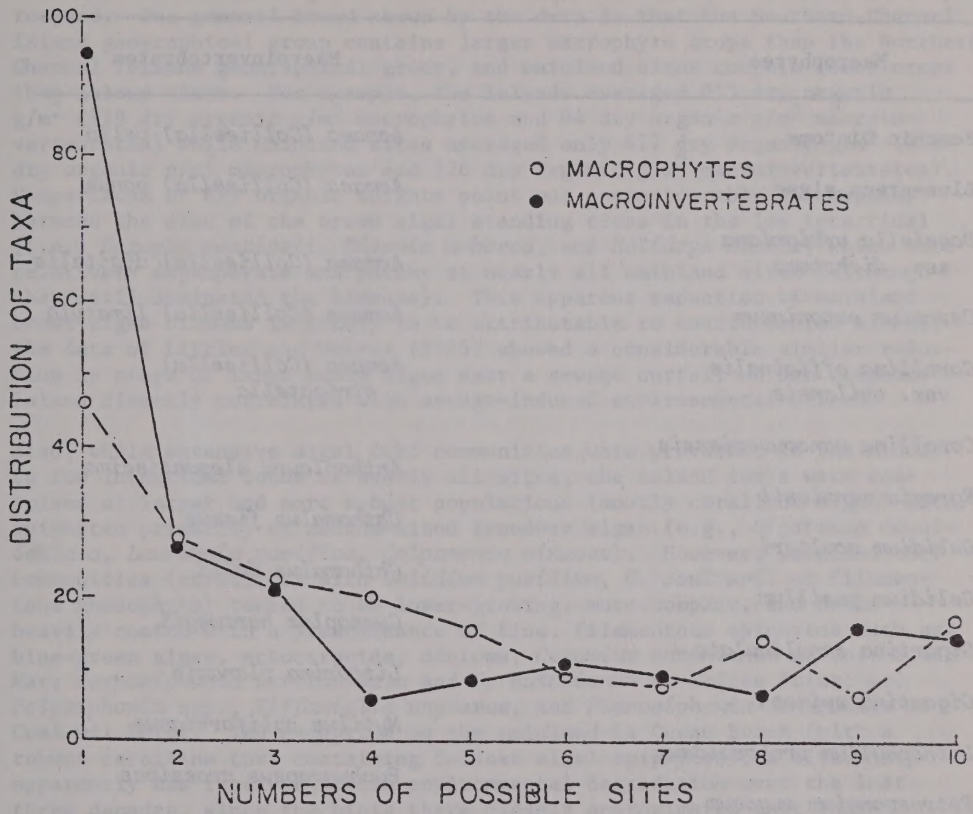


Figure III.C-17 Uniqueness of Taxa Shown by Their Distribution as a Function of the Number of Sites in Which They Occurred.

Source: Littler (1977).

Table III.C-6

SPECIES COMMON TO ALL 10 SITES

Macrophytes	Macroinvertebrates
Benthic Diatoms	*Acmaea (Collisella) pelta*
Blue-green algae	*Acmaea (Collisella) conus*
Bossiella orbigniana ssp. *dichotoma*	*Acmaea (Collisella) digitalis*
Ceramium eatonianum	*Acmaea (Collisella) limatula*
Corallina officinalis var. *chilensis*	*Acmaea (Collisella) strigatella*
Corallina vancouveriensis	*Anthopleura elegantissima*
Egregia menziesii	*Chthamalus fissus*
Gelidium coulteri	*Chthamalus dalli*
Gelidium pusillum	*Cyanoplax hartwegii*
Gigartina canaliculata	*Littorina planaxis*
Gigartina spinosa	*Mytilus californianus*
Lithophyllum proboscideum	*Pachygrapsus crassipes*
Petrospongium rugosum	*Pugettia producta*
Pterocladia capillacea	*Tetraclita squamosa rubescens*
Pterosiphonia dendroidea	

Source: Littler (1977).

systems with stations having well developed high intertidal faunal assemblages. The grand totals and means of all parameters measured were summed and averaged for the six island sites and four mainland sites, respectively. The island sites had higher values than the mainland sites in nearly every respect. One general trend shown by the data is that the Southern Channel Island geographical group contains larger macrophyte crops than the Northern Channel Islands geographical group, and mainland sites contain lower crops than island sites. For example, the islands averaged 813 dry organic g/m^2 (719 dry organic g/m^2 macrophytes and 94 dry organic g/m^2 macroinvertebrates) while mainland sites averaged only 477 dry organic g/m^2 (351 dry organic g/m^2 macrophytes and 126 dry organic g/m^2 macroinvertebrates). Comparisons of dry organic weights point out a considerable discrepancy between the size of the brown algal standing crops in the low intertidal (i.e., *Egregia menziesii*, *Eisenia arborea*, and *Halidrys dioica*) which were relatively depauperate and patchy at nearly all mainland sites (although they still dominated the biomass). This apparent reduction of mainland brown-algae biomass is likely to be attributable to environmental stress; the data of Littler and Murray (1975) showed a considerable similar reduction in crops of large brown algae near a sewage outfall on San Clemente Island directly correlated with sewage-induced environmental stress.

Also, while extensive algal turf communities were prevalent in the middle to low intertidal zones at nearly all sites, the island turfs were comprised of larger and more robust populations (mostly coralline algae) with epiphytes primarily of medium-sized frondose algae (e.g., *Gigartina canaliculata*, *Laurencia pacifica*, *Colpomenia sinuosa*). However, mainland turf communities (corallines with *Gelidium pusillum*, *G. coulteri*, or filamentous Rhodophyta) tended to be lower-growing, more compact, and often heavily coated with a predominance of fine, filamentous epiphytes such as: blue-green algae, ectocarpoids, diatoms, *Ceramium eatonianum* at Corona del Mar; *Herposiphonia verticillata* and *C. eatonianum* at Whites Point; and *Polysiphonia* spp., *Tiffaniella snyderae*, and *Pterosiphonia dendroidea* at Coal Oil Point. The exception on the mainland is Ocean Beach (with a robust coralline turf containing foliose algal epiphytes), a site that apparently has received little environmental degradation over the last three decades, since the biota there closely approximates that found (Stephenson and Stephenson, 1972) at nearby Bird Rock and a rocky platform north of Scripps pier during 1947. The only island site with a community of fine, filamentous forms (*C. eatonianum* and *Centroceras clavulatum*) epiphytic on *Corallina* turf (*C. officinalis* var. *chilensis* and *C. vancouveriensis*) was San Nicolas Island which received considerable perturbation by sand inundation. Therefore, it is suggested that the highly epiphytized, compact turf morphology, characterized by algal populations having relatively great surface area to weight ratios, high reproductive capacities, high growth rates, simple thallus forms, and mechanisms for short and simple life histories, may be characteristic of communities in stressed environments. Such populations may, in fact, comprise intermediate seral communities maintained in disclimax by lack of environmental constancy and/or pollution stress.

Other parameters for which islands exceeded mainland sites were the following: number of taxa (islands 145, mainland 134), richness (islands D' of 21.90, mainland 18.62) evenness (islands J' of 0.60, mainland 0.58), and Shannon-Weaver diversity (islands H' of 2.74, mainland 2.54).

One important consideration involves the lack of a large difference between overall macrophyte cover on islands (80%) compared to mainland sites (80%). Average macroinvertebrate cover on islands was not much greater than on mainland sites (16% vs. 13%), but average macroinvertebrate density was considerably lower at mainland sites (2,024 individuals/m^2) than on islands (2,472/m^2).

Several workers (i.e., Dawson, 1959, 1965; Nicholson and Cimberg, 1971; Widdowson, 1971; Thom, 1976) have documented large reductions in the number of macrophytic species over time attributable to human influences (e.g., pollution) on the Southern California mainland. Littler found contrastingly, that the average number of macrophyte species occurring in sample plots at the six relatively unpolluted island sites (72) was nearly equal to the average number at the mainland sites (71). If it can be assumed that the islands have remained relatively unpolluted and that they historically contained roughly at least as many species as the mainland (both highly likely), then this similarity of species numbers (72 vs. 71) could lead to the interpretation that many if not most of the species recorded as "lost" due to pollution on the mainland by the above authors must have been rare or uncommon forms that would not be likely to be found even by Littler's extensive quadrat sampling. Another more probable interpretation (aside from some very trivial ones) is that the transect sampling procedures used first by Dawson (1959) on the mainland (i.e., techniques that are appropriate for the measure of abundance (cover or frequency) but which were used instead to report presence and absence of taxa) were such that only very abundant species could be recorded. This would seem to be the case because Littler's methods (which also were not designed to "find" species but to measure distributional patterns) were considerably more effective in recording greater numbers of macrophyte taxa present at Corona del Mar, Coal Oil Point, and Whites Point than did either Dawson (1959, 1965) or Nicholson and Cimberg (1971). Thus, if human effects caused declines but not disappearances (our data contrasting island with mainland biomass show this to be a likely case), subsequent use of the Dawson method would encounter fewer species, although the original number could still be present in the area. It is likely that both of the above phenomena (that is, declines in abundance and actual loss of rare forms) explain the results recorded by workers who repeated Dawson's (1959) original sampling methods.

Some (but not many) of the differences found between island and mainland community parameters (e.g., total species numbers, richness, evenness, and Shannon-Weaver diversity) can be attributed to the absence of samples from the sand-inundated high-intertidal habitat, which is usually dominated by animals, at three of the four mainland sites. On the other hand, the

absence of a high intertidal zone makes the lower values of overall mean macrophyte dry organic biomass and macrophyte cover for mainland sites even more striking, because only the low to middle zones (which normally contain the bulk of the macrophyte crops) were sampled.

Mussel Beds. Straughan and Kanter (1977) conducted a three-dimensional study of mussel (*Mytilus californianus*) communities at six locations in the California Bight (Figure III.C-18) which included two mainland locations (Coal Oil Point and Ocean Beach, San Diego) and four island sites (San Miguel, Santa Cruz, San Nicolas and Santa Barbara Islands).

Biomass measurements, as was obvious, indicated molluscs, mainly mussels, composed over 90 percent of the total biomass from the mussel bed. All other phyla combined accounted for 10 percent or less of the total biomass. Mussels dominated the biomass because of their large size compared to the other inhabitants. The mussels were not numerically dominant and were out-numbered by many other organisms within the mussel bed, including barnacles, amphipods, small bivalves and nematodes. The size and weight of the mussels varied from one locality to another. The largest and heaviest mussels were collected from Coal Oil Point and San Nicolas Island, and the smallest (lightest) mussels were collected from Santa Barbara Island and San Diego. The biomass at each area showed little variation between collection throughout the year. This was a reflection of the lack of variability in the biomass of the dominant mussels.

Kanter indicated biomass data were of limited value because lumping all members of a phylum together masked any trophic distinctions between species.

The mussel beds surveyed during this study supported an extremely rich fauna. Together they contained (conservatively) 346 species from twelve phyla. The lowest number of species from a single set of samples (1,500 cm^2) was 41 (San Miguel Island) and the highest was 78 species (Santa Cruz Island). This high number of species probably exists due to the three dimensional structure of the mussel beds.

Three phyla, the Annelida, Mollusca, and Arthropoda, combined to contribute over 70% of the mussel community species. These organisms occupy a wide range of habitats within the mussel bed and exploit an equal variety of food resources. However, the natural history of most species found in the mussel bed remains unknown, and their respective niches for exploitation of food and habitat resources, in many cases, can only be inferred from consideration of morphological characteristics.

Several species index or species index related measurements were taken, causing Kanter to conclude the more informative and economical measure of diversity appears to be species counts (species diversity). The presence of an animal, regardless of its numerical abundance, implies its occupation of an ecological niche. This means that a multi-dimensional resource state is being exploited by the animal and thus the resource state exists by definition. The principle that no two species can occupy the same

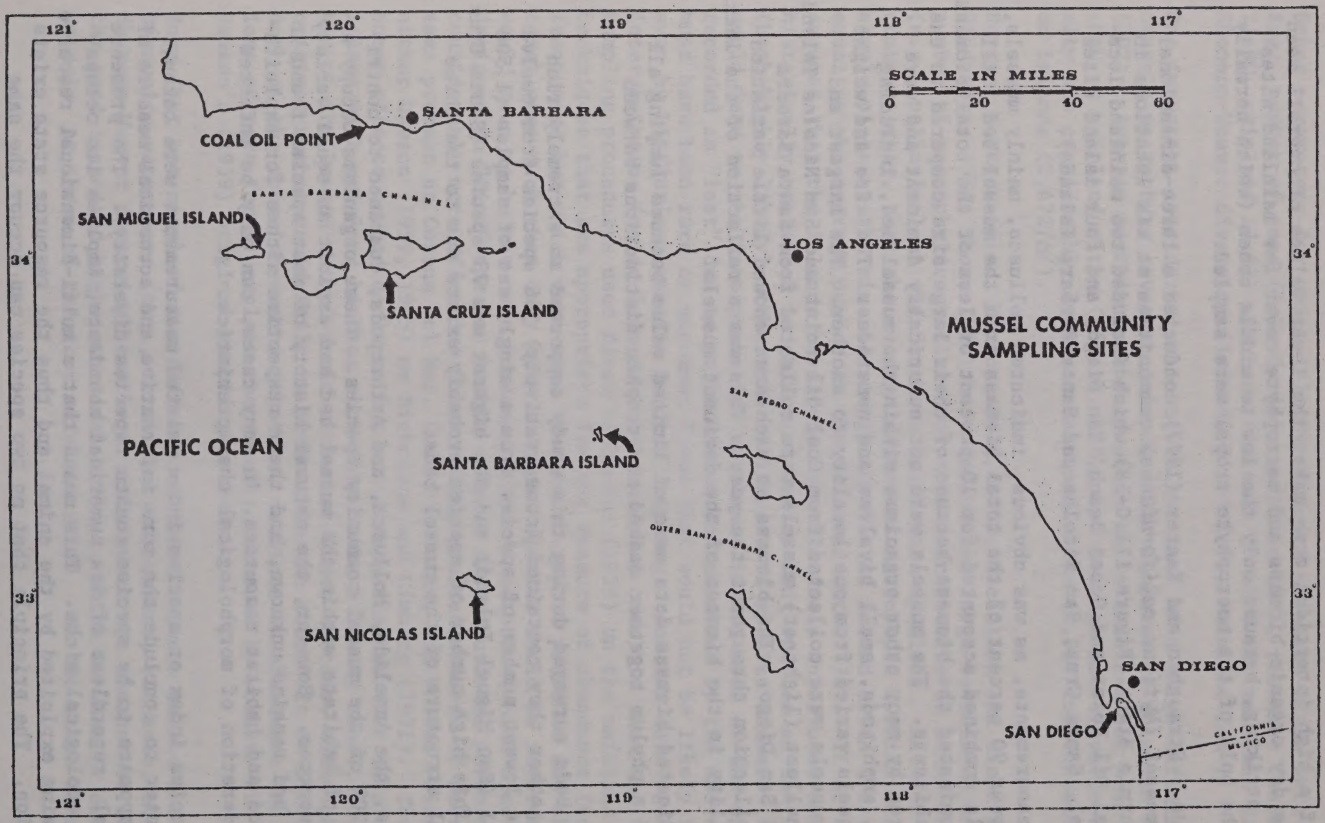


Figure III.C-18. Mussel Community Sampling Sites (1975-1976).

Source: Kanter (1977).

niche (Volterra, 1926) suggests that a more diverse fauna exploits an area with a greater diversity of resources.

Those diversity measures which calculate the percentage composition by numbers of the various species present in a sample, e.g., Shannon-Weiner index (H'), are referred to as dominance diversity indices. Dominance diversity indices are based on information theory and have as their basic premise: the more the constituent species are represented by equal numbers of individuals, the more diverse the fauna. Diversity measured by counting the number of species is referred to as species diversity and has as its basic premise: the more species, the more diverse the fauna. Dominance diversity indices (H') are actually composite measures incorporating both species richness (R) and evenness (J') into a single measure. It is difficult to interpret dominance diversity alone because the two subcomponents (J' and R) may contribute differently to the diversity value. This may result in areas with equal values of H' for entirely different species compositions.[a]

Santa Cruz Island was the most diverse locality sampled (Table III.C-7). The species diversity (74) and dominance diversity index (H' = 2.828) were high and reflected the large number of species which the mussel bed supported. The species evenness (J' = 0.657) and richness (R = 7.986) were also high, and both contributed to the high dominance diversity index.

Coal Oil Point samples displayed the second highest species diversity with 73 species (Table III.C-7). However, the dominance diversity index (H' = 1.622) did not reflect this high number of species. The low evenness (J' = 0.379) of species abundance was responsible for this incongruity, in spite of the moderately high species richness (R = 6.666). Although Coal Oil Point and Santa Cruz Islands had essentially the same number of species (73 versus 74 respectively), the dominance diversity values (H') shown in Table III.C-7 do not reflect this similarity.

The Santa Barbara Island mussel bed had a high species diversity (65 species). The dominance diversity index reflected this with a value of H' = 2.608. The relatively high values for both richness (R = 7.532) and evenness (J' = 0.628) contributed to this high dominance diversity value. The dominance diversity value for the Santa Barbara Island samples was much higher than that for the Coal Oil Point samples in spite of the high species diversity from Coal Oil Point. Again, this was a result of the evenness measure which was very low for Coal Oil Point.

San Nicolas Island and San Miguel Island samples had similar species diversities (55 and 51 species respectively) and dominance diversities (H' = 2.313 and 2.379 respectively). In addition, their richness and evenness values were comparable. This consistency in all measures was rare, and due in part to averaging the measures for all collections (Table III.C-7). In spite of this, mussel beds from both of these sites appear equally diverse.

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[a]Note that all values discussed in this section are average values.

Table III.C-7

A SUMMARY OF TOTAL NUMBER OF SPECIES, SPECIES DIVERSITY (H'), SPECIES EVENNESS (J') AND SPECIES RICHNESS (R) FOR ALL MAINLAND AND ISLAND COLLECTIONS

SITE: San Nicolas Island

Quarter	Cumulative Number of Species	Diversity (H')	Species Evenness (J')	Species Richness (R - Gleason)
1	49	2.014	0.517	5.971
2	53	2.274	0.573	5.575
3	53 (81)[a]	2.005 (1.856)[a]	0.505 (0.422)[a]	5.560 (7.182)[a]
4	63 (75)[a]	2.959 (3.011)[a]	0.714 (0.697)[a]	8.262 (9.239)[a]
AVERAGE	55 (78)[a]	2.313 (2.433)[a]	0.577 (0.559)[a]	6.342 (8.210)[a]

SITE: Coal Oil Point

Quarter	Cumulative Number of Species	Diversity (H')	Species Evenness (J')	Species Richness (R - Gleason)
1	70	1.780	0.419	6.847
2	—	———	———	———
3	75	1.464	0.339	6.485
4	—	———	———	———
AVERAGE	73	1.622	0.379	6.666

Table III.C-7 (Cont'd.)

SITE: San Miguel Island

Quarter	Cumulative Number of Species	Diversity (H')	Species Evenness (J')	Species Richness (R - Gleason)
1	—	———	———	———
2	41	1.764	0.475	4.336
3	55	2.350	0.587	5.810
4A	55	2.674	0.667	7.100
4B	51	2.727	0.693	6.883
AVERAGE	51	2.379	0.606	6.032

SITE: Santa Barbara Island

Quarter	Cumulative Number of Species	Diversity (H')	Species Evenness (J')	Species Richness (R - Gleason)
1	56	2.300	0.571	6.376
2	74	3.081	0.716	9.117
3	73	2.096	0.489	7.604
4	55	2.953	0.737	7.031
AVERAGE	65	2.608	0.628	7.532

Table III.C-7 (Cont'd.)

SITE: San Diego

Quarter	Cumulative Number of Species	Diversity (H')	Species Evenness (J')	Species Richness (R - Gleason)
1	48	2.415	0.624	5.724
2	—	—	—	—
3	43	1.099	0.292	4.395
4	—	—	—	—
AVERAGE	46	1.757	0.458	5.060

SITE: Santa Cruz Island

Quarter	Cumulative Number of Species	Diversity (H')	Species Evenness (J')	Species Richness (R - Gleason)
1	74	2.769	0.643	7.929
2	78	2.770	0.636	7.834
3	69	2.473	0.584	7.153
4	75	3.299	0.764	9.028
AVERAGE	74	2.828	0.657	7.985

Source: Straughan and Kanter, 1977.

San Diego mussel beds supported the lowest species diversity (46). The dominance diversity index was also low (H' = 1.757). This low dominance diversity was a result of the low richness and evenness values (Table III.C-7). The low dominance diversity for San Diego samples was still higher than that from Coal Oil Point samples, because of the low evenness of Coal Oil Point samples.

The results discussed above suggest that the measurement of dominance diversity alone does not represent the diversity of an area. The component measures of richness and evenness are needed to interpret dominance diversity in a comparison of areas.

Kanter questions the value of using evenness in the measurement of diversity because trophic distinctions are masked by it. Conversely, a low evenness may reflect environmental purturbations of the area allowing a limited number of species to exist "comfortably" in relatively high numbers while others to occur only in low numbers, perhaps even accidently, because environmental stress is too severe to support significant populations.

The most informative results were obtained from community classification analysis and discriminant analysis.

Mussel Community Classification Analysis. The classification analyses of the mussel bed community revealed three major patterns. The patterns corresponded to unique species assemblages associated with the different geographic mussel bed samples. These included:

- Species groups ubiquitous in all mussel beds examined.
- Species groups which distinguished island from mainland mussel beds.
- A unique species assemblage from San Miguel Island that distinguished this area from the other island localities.

The classifications of the first and third quarter collections (Figures III.C-19 and 21) contained data from both mainland and island localities. The ubiquitous species groups were E (Figure III.C-19 and Legend), B and F (Figure III.C-21 and Legends). The species included in these groups were quite comparable overall and were predictable occupants of any mussel beds sampled from the Southern California area. These species included the sea anemone *Anthopluera xanthogrammica*, the gooseneck barnacle *Pollicipes polymerus*, the bivalve *Septifer bifurcatus*, the nemertean *Emplectonema gracile*, the gastropod *Tegula funebralis* and the limpet *Collisella strigatella (= Acmaea strigatella)*. *A. canthogrammica* is possibly the same species as *A. elegantissima* reported by Littler, et al., (1977).

The classifications of the second and fourth quarter collections (Figures III.C-20 and III.C-22) included data from island localities only and produced similar ubiquitous species groups, D (Figure III.C-20 and Legend) and E (Figure III.C-22 and Legend). The ubiquitous species for the island localities alone included the species mentioned above (from both mainland

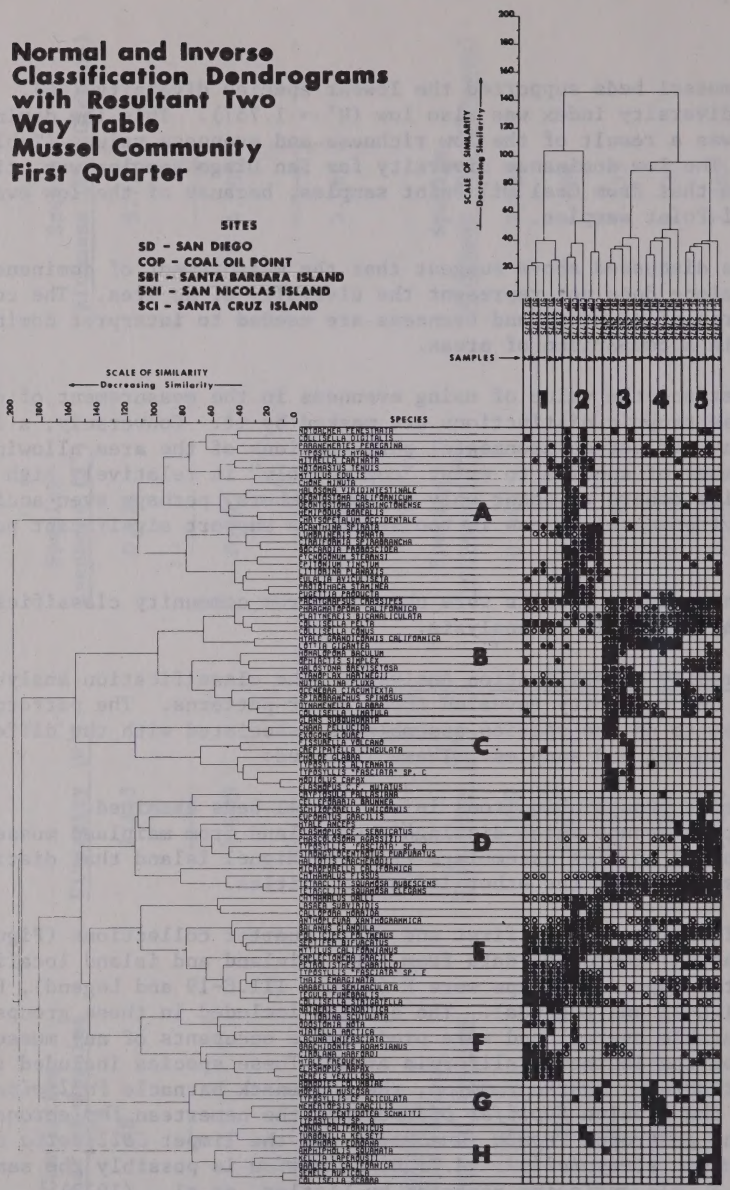


Figure III.C-19 First Quarter Classification Dendrograms With Resultant Two-Way Table Symbols Represent Relative Species Abundance in Percent of Maximum Abundance: 0= 1-25%, ◐ = 26-50%, ● = 51-75%, ■ = 76-100%.

Source: Straughan and Kanter, 1977.

Legend for Figure III.C-19

GROUP E FROM CLUSTER ANALYSIS OF FIRST QUARTER
MUSSEL COMMUNITY STUDY

Chthamalus dalli barnacle

Lasaea subviridis

Callopora morrida

Anthopleura xanthogrammica sea anemone

Balanus glandula barnacle

Pollicipes polymeras goose neck barnacle

Septifer bifurcatus bivalve

Mytilus californianus mussel

Emplectonema gracile nemertean

Petrolisthes cabrilloi

Typosyllis fasciata sp. E

Thais emarginata

Arabella semimaculata polychaete

Tegula funebralis

Collisella strigatella (= Acmaea)

Source: Straughan and Kanter, 1977.

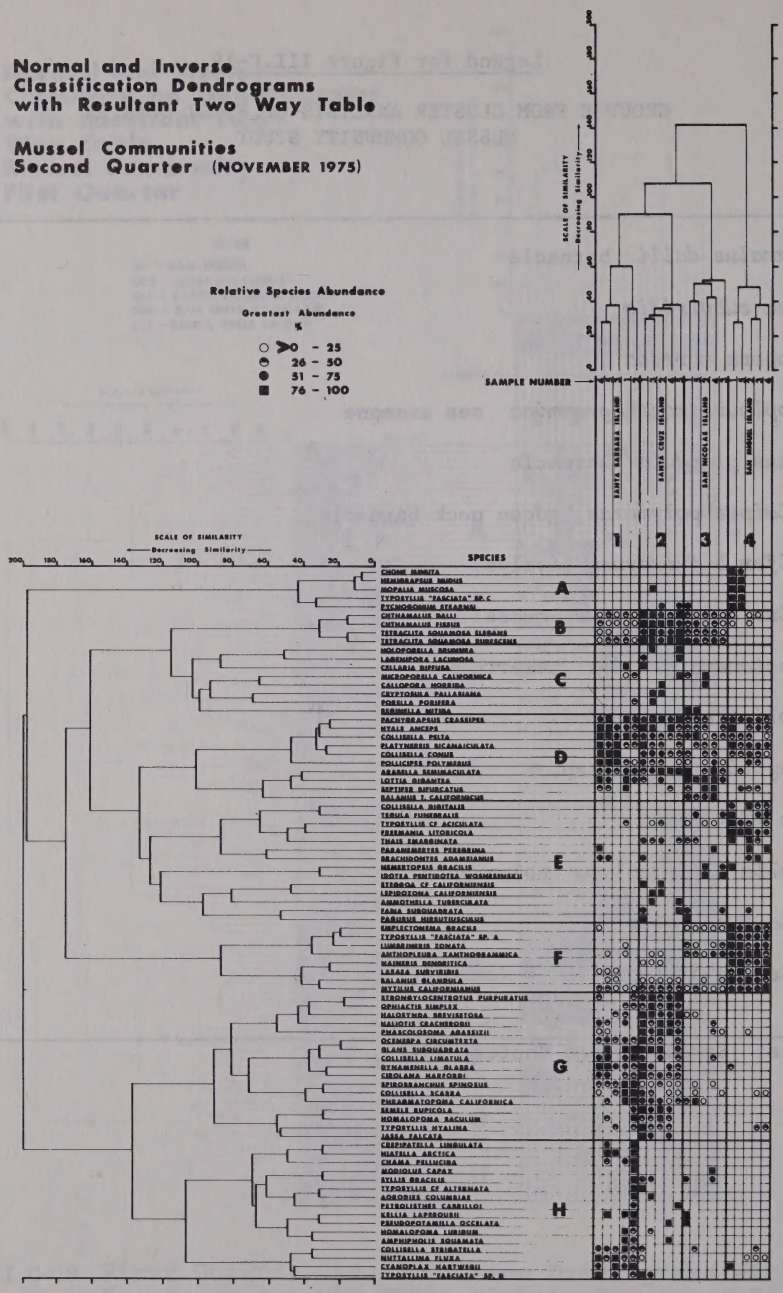


Figure III.C-20 Second Quarter Classification Dendrograms With Resultant Two-Way Table.

Source: Straughan and Kanter, 1977.

Legend for Figure III.C-20

GROUP D FROM CLUSTER ANALYSIS OF SECOND QUARTER (NOVEMBER 1975)
MUSSEL COMMUNITY STUDY

Pachygrapsus crassipes

Hyale anceps

Collisella pelta (= Acmaea)

Pollicipes polymerus

Collisella conus (= Acmaea)

Platynereis bicanaiculata

Arabella semimaculata

Lottia gigantea

Septifer bifurcatus

Balanus t. californicus

Source: Straughan and Kanter, 1977.

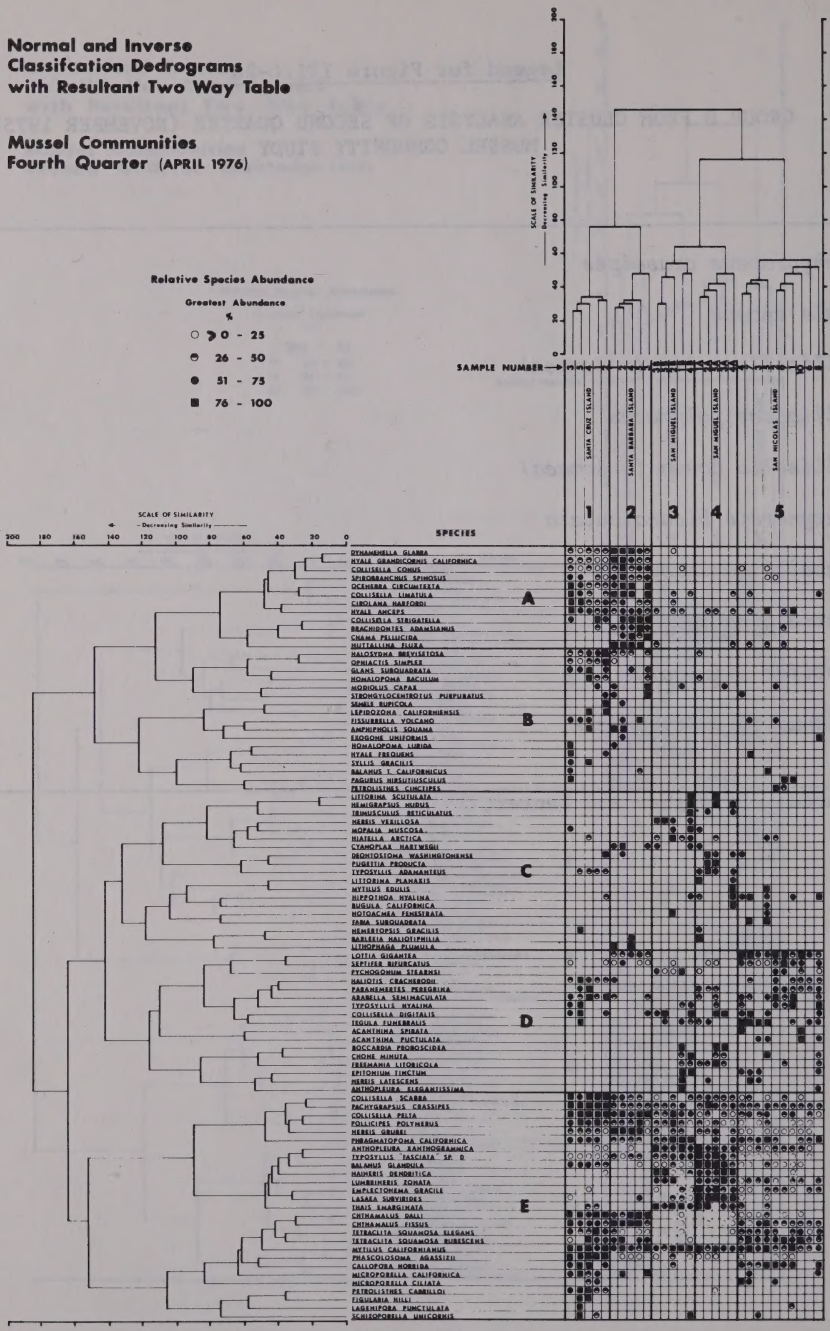


Figure III.C-21 Fourth Quarter Classification Dendrograms With Resultant Two-Way Table.

Source: Straughan and Kanter, 1977.

Legend for Figure III.C-21

GROUP B FROM CLUSTER ANALYSIS OF FOURTH QUARTER (APRIL 1976)
MUSSEL COMMUNITY STUDY

Microporella californica

Lagemipora punctulata

Tetraclita squamosa elegans barnacle

Tetraclita squamosa rubescens

Chthamalus dalli

Chthamalus fissus

Schizoporella unicornis

Celleporaria brunnea

Callopora horrida

Hippothoa hyalina

Lasaea subvirdis

Cryptosula pollasiana

Source: Straughan and Kanter, 1977.

Legend for Figure III.C-21

GROUP F FROM CLUSTER ANALYSIS OF FOURTH QUARTER (APRIL 1976)
MUSSEL COMMUNITY STUDY

Lumbrineris zonata

Anthopleura xamthogrammica

Septifer bifurcatus

Collisella strigatella (= Acmaea)

Tegula funebralis

Arabella iricolor

Collisella pelta (= Acmaea)

Nereis grubei

Pollicipes polymerus

Cirolama harfordi

Phascolosoma agassezii

Myale anceps

Typostyllis "fasciata" sp. D

Emplectonema gracile

Balanus glandula

Mytillus californianus

Source: Straughan and Kanter, 1977.

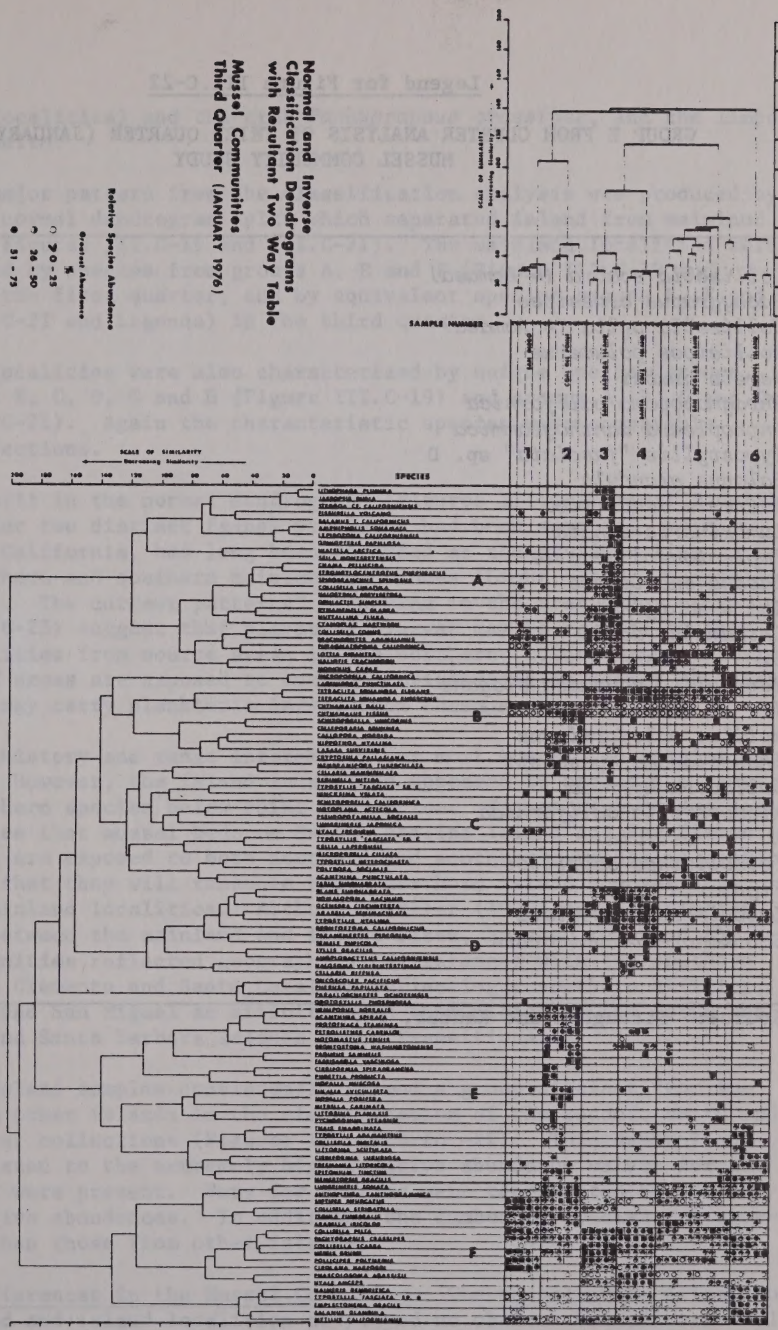


Figure III.C-22 Third Quarter Classification Dendrograms With Resultant Two-Way Table.

Source: Straughan and Kanter, 1977.

Legend for Figure III.C-22

GROUP E FROM CLUSTER ANALYSIS OF THIRD QUARTER (JANUARY 1976)
MUSSEL COMMUNITY STUDY

Collisella scabra (= Acmaea)
Pachygrapus crassipes
Collisella pelta (= Acmaea)
Pollicipes polymerus
Nereis grubei
Phragmatopoma californica
Anthopleura xanthogrammica
Typostyllis "fasciata" sp. D
Balanus glandula
Naineris dendritica
Lumbrineris zonata
Emplectonema gracile
Lasaea subvirides
Thais emarginata
Chthamalus dalli
C. fissus
Tetraclita squamosa elegans
T. s. rubescens
Mytilus californianus
Phoscolosoma agassizii
Collopora horrida
Microporella californica
M. ciliata
Petrolisthes cabrilloi
Figularia milli
Lagenipora punctulata
Schizoporella unicornis

Source: Straughan and Kanter, 1977.

and island localities) and the crab *Pachygrapsus crassipes*, and the limpet *Collisella pelta*.

The second major pattern from the classification analysis was produced by the primary normal dendrogram split which separated island from mainland localities (Figures III.C-19 and III.C-21). The mainland localities were characterized by species from groups A, E and F (Figure III.C-19 and Legends) in the first quarter, and by equivalent species groups B, E and F (Figure III.C-21 and Legends) in the third quarter.

The island localities were also characterized by unique species groups. These groups B, C, D, G and H (Figure III.C-19) and groups A, B, C and D (Figure III.C-21). Again the characteristic species were comparable between collections.

The major split in the normal dendrograms (Figures III.C-19 and III.C-21) suggested that two distinct faunal provinces had been sampled. Point Conception, California, has long been regarded as the dividing line between northern and southern mainland provinces (Light, 1970; Johnson and Snook, 1967). The current patterns[a] occurring in the area under study (Figure III.C-23) suggest that planktonic larvae may be carried to the island localities from source areas in the northern (colder water) province. The mainland areas are exposed to currents originating in warmer southern areas which may carry planktonic larvae from these areas.

The natural history and range information for most mussel bed species is incomplete. However, the island localities appeared to extend the range of many northern species below Point Conception. Kanter recommended for future studies that mussel beds on Santa Catalina Island and San Clemente Island which are exposed to both northern and southern currents be examined. He predicts that they will resemble their northern island counterparts more than mainland localities. Although Littler (1977) noted a similar difference between the mainland and island sites, he also reported the island communities reflected geographical differences with the southern islands, San Clemente and Santa Catalina reflecting a southern affinity, San Nicolas and San Miguel an affinity with communities to the north and Santa Cruz and Santa Barbara Islands being transitional.

San Miguel Island samples consistently formed a group distinct from the samples from other islands in the classification of the second, third and fourth quarter collections (Figures III.C-20 to -22). This separation appeared related to the extremely high relative abundance values for the species that were present. Very few species were represented by low or medium relative abundances. In addition, the number of species was somewhat lower than those from other islands.

Seasonal Differences in the Mussel Community. The mussel communities from both mainland and island localities displayed no obvious overall seasonal

[a]Note that these are generalized current patterns in selected areas which may receive waters from northern and southern areas.

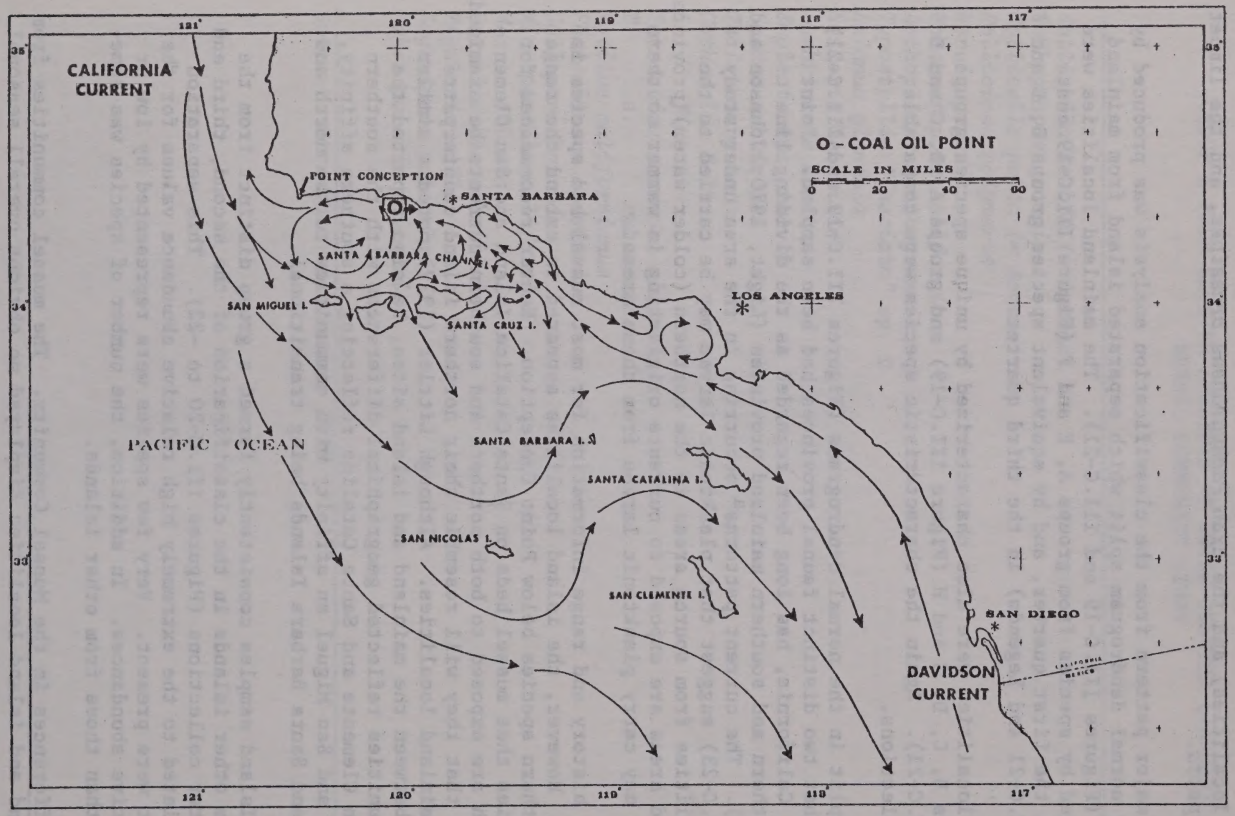


Figure III.C-23 Generalized Current Patterns of the Pacific Ocean from Point Conception to San Diego, California.

Source: Kanter (1977).

changes. Ubiquitous species common to all mussel beds in the classification analyses remained relatively constant in numbers throughout the year. Species groups which characterized specific localities only changed slightly in composition throughout the year. Those changes which usually occurred were the result of relative abundance changes. These relative abundance changes may indicate seasonal differences, but at the present time these differences cannot be distinguished from abundance differences which result from the influence of local factors like intertidal height.

Detailed studies of the species in question at specific localities are necessary to distinguish between actual seasonal changes in abundance and those which result from sampling procedures.

The Effect of Intertidal Height on Mussel Community Composition. The effect of relative intertidal height differences on local species abundances was investigated during the fourth quarter collections at San Miguel Island.

In general, the mussel bed inhabitants displayed higher abundances in the upper collection than in the lower collection at San Miguel Island. However, those collections did not represent extremes in intertidal height of the mussel bed. It was suggested that collections from extremes in intertidal height will exhibit greater abundance differences as well as species composition differences and should be investigated further.

Summary. *Mytilus californianus* communities (mussel beds) were examined from six geographic localities in Southern California. These included two mainland sites, Coal Oil Point and San Diego; and four island sites, San Miguel, Santa Cruz, San Nicolas, and Santa Barbara Islands. Optimal sample sizes were determined for each locality. In general, a sample size of 1,500 cm^2 (five cores) was optimal for the "typical" mussel bed. However, structurally unique mussel beds required individual consideration. Community biomass, diversity, species richness, and species evenness were calculated quarterly for the island localities and biannually for mainland locations. The molluscs, primarily the mussels, accounted for 90% of the total biomass, while all other groups combined accounted for 10% or less of the total biomass. The mussel communities from all localities contributed to the master species list which conservatively contained 346 species. The most diverse localities were Coal Oil Point and Santa Cruz Island with an average number of 73 and 74 species 0.5 m^2, respectively. No overall seasonal patterns existed in community composition. The community similarity analyses showed the mainland localities biotically dissimilar from the islands and both groups were characterized by distinct faunal assemblages. In addition, San Miguel Island biota were unique among the island sites. The most important mussel bed structural attributes provided habitats for the associated community and included sediment and coarse fraction features. Food-related resources provided by the mussel bed were secondarily important. Community diversity generally increased with the quantity of habitat and food resources.

Mussel Community Discriminant Analysis. Multiple discriminant analysis was employed to identify the most important abiotic factors associated with mussel community differences. Twelve environmental variables related to food, habitat and shelter provided by the mussel bed were measured during this study and were included in the discriminant analysis. Some of these variables provided combinations of resources for selected mussel community species, e.g., sediment provided both habitat and food for some deposit feeding polychaetes. The analysis constructed discriminant axes from linear combinations of these variables which best separated predefined groups. The predefined groups in this case were the site groups from the normal classification.

The most important variables were principally habitat-related. These included sediment size and quantity for the first quarter collections. Sediment provided substrate for many phyla, including polychaetes and molluscs, two of the dominant groups within the mussel bed. Therefore, it was not surprising to find a relationship between the quantity of this factor (substrate) and the total number of species. Additional habitat-related variables included qualitative characteristics of the sediment, e.g., sediment kurtosis. This feature of the sediment in part described the heterogeneity of the substrate, and although it did not correlate directly with species diversity differences, it was important in group separations. Other important habitat-related variables included the quantity of coarse fraction material and coarse fraction pore base. These variables provided interstitial habitat "holes" for organisms and surfaces for attachment. Again, members of the dominant groups, arthropods, molluscs and tube-building polychaetes, exploited these habitats.

Food-related variables were of secondary importance in group separations. Usually they separated groups on axes after initial separation by habitat-related variables. The quantity of detritus was important and generally an inverse relationship existed between the species diversity and the quantity of detritus. However, this was not a consistent relationship. The quantity of detritus was expected to correlate directly with the species diversity, providing food for a variety of opportunistic (scavenger) species or a substrate for bacterial growth which could serve as a food source; however, this was not a consistent relationship.

The mussel bed insulated the associated community against various forms of environmental stress like extreme temperature changes. Depending on the time of day and prevailing climatic conditions, the ambient air and surface mussel bed temperatures exceeded internal mussel bed temperatures (Figure III.C-24). The mussel bed also insulated against wave and surf action. These insulating properties, considered collectively, provided shelter for the mussel community. Mussel bed thickness was an indirect measure of this shelter variable and was considered in the discriminant analysis. Although the shelter aspect is obviously important, this variable did not dominate any discriminant axes. This probably reflected the consistency of this among the different mussel beds.

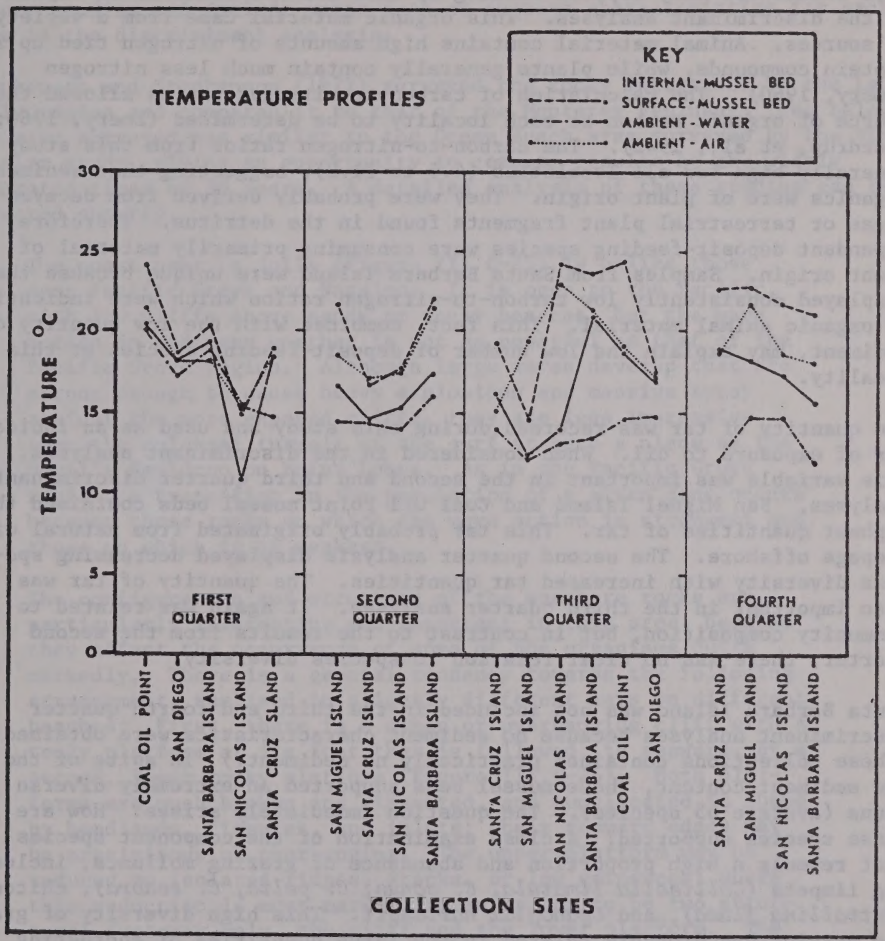


Figure III.C-24 Temperature Profiles For All Collection Sites.

Source: Straughan and Kanter, 1977.

Organic material contained in the mussel bed sediments was a potential food source for many deposit-feeding species and was found to be important in the discriminant analyses. This organic material came from a variety of sources. Animal material contains high amounts of nitrogen tied up in protein compounds, while plants generally contain much less nitrogen (Emery, 1960). The calculation of carbon-to-nitrogen ratios allowed the source of organic carbon at each locality to be determined (Emery, 1960; Sverdrup, et al,, 1942). The carbon-to-nitrogen ratios from this study were generally high for all localities (4.6 to 11.3), suggesting that sediment organics were of plant origin. They were probably derived from decayed algae or terrestrial plant fragments found in the detritus. Therefore, dependent deposit-feeding species were consuming primarily material of plant origin. Samples from Santa Barbara Island were unique because they displayed consistently low carbon-to-nitrogen ratios which were indicative of organic animal material. This fact, combined with the low quantity of sediment, may explain the low number of deposit-feeding species at this locality.

The quantity of tar was recorded during this study and used as an indicator of exposure to oil. When considered in the discriminant analysis, this variable was important in the second and third quarter discriminant analyses. San Miguel Island and Coal Oil Point mussel beds contained the highest quantities of tar. This tar probably originated from natural oil seepage offshore. The second quarter analysis displayed decreasing species diversity with increased tar quantities. The quantity of tar was also important in the third quarter analyses. It again was related to community composition, but in contrast to the results from the second quarter, there was no clear relation to species diversity.

Santa Barbara Island was not included in the third and fourth quarter discriminant analyses because no sediment characteristics were obtained. (These collections contained practically no sediment.) In spite of the low sediment content, these mussel beds supported an extremely diverse fauna (average 65 species). The question immediately arises: How are these species supported? A close examination of the component species list reveals a high proportion and abundance of grazing molluscs, including limpets (*Collisella limatula, C. conus, C. pelta, C. scabra*), chitons (*Nuttallina fluxa*), and *Cyanoplax hartwegii*. This high diversity of grazing species was probably related to the large quantities of encrusting algae found at this locality. In addition, the extremely pitted substrate of this area provided habitats (e.g., for the chitons) beneath the sheltering mussel bed.

The major dendrogram divisions in the first and third quarter classifications (Figures III.C-19 and 21) separated the islands from mainland sites. As discussed earlier, the community differences probably corresponded to differences in the planktonic larval source areas. The planktonic larvae recruited to the Channel Island localities were apparently carried by currents and water masses arising north of Point Conception, and those settling at mainland localities were probably carried by southern warm-water currents. This information has been inferred from knowledge of the

northern and southern faunas, as well as available hydrographic charts (Figure III.C-23). It would be desirable to quantify this information for future studies and include water mass or current characteristics for each site in the discriminant analysis.

Stephenson and Stephenson (1972) surveyed the rocky intertidal in the La Jolla region and compared it to that of the Monterey Peninsula (see below). The area surveyed was similar to the Ocean Beach area surveyed by the BLM Littler study, giving an opportunity to compare results at the widely separated times of 30 years. A detailed analysis of these studies can be expected shortly.

> The coast near La Jolla (Figure III.C-25) is unlike those near Pacific Grove and Nanaimo. It is open to the Pacific, with low cliffs above sandy or rocky beaches, but the wave action in ordinary weather is not as powerful as that of the Pacific Grove region. Although large waves develop that are strong enough to cause heavy explosions and massive spray against the more exposed cliffs, they are less impressive than the colossal turmoil of the surf at such a place as the Devil's Cauldron on Point Lobos. As in the Pacific Grove region, a transition in the population of a given zone occurs between those rocks on which the wave action is strongest and those on which it is weakest.
>
> The configuration and structure of the seashore rocks are particularly interesting and important in this area, because they affect the occurrence of some of the organisms quite markedly. There is a general tendency towards the following arrangement, realised in slightly different ways on different beaches: First, there is a steep or overhanging cliff with a rocky platform at its foot that is followed, to seaward, by a second, lower rocky platform (Figure III.C-26). Both platforms are much broken and dissected, and complicated in shape by headlands, fissures, and inlets; their seaward edges may be precipitous or overhanging. The upper platform may be reduced to isolated ridges, stacks, or low eminences; where this reduction is most marked, there appear to be two structural features only, the cliff and the lower platform. The lower platform is submerged even by the minimal high and low waters, whereas the highest parts of the upper platform are not completely submerged even at the higher high waters, though they are commonly wetted completely by surge or spray. The foot of the cliff may be submerged at high water, and the face of the cliff, where it is most exposed to the waves, may be thoroughly drenched by spray. Apart from the main sandy beaches, which are typically free from rocks, there may be small stretches of sand or pebbles behind the reef at the foot of the cliff. Boulders are plentiful, either scattered on the reef, in pools, and in creeks, or in definite concentrations, perhaps at the foot of the cliff or sloping shore, or at the seaward edge of the rocks.

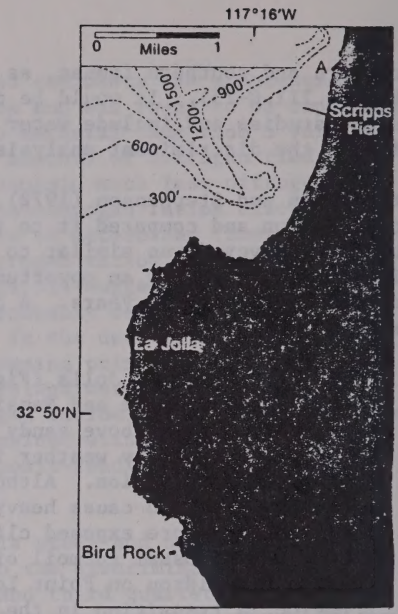


Figure III.C-25

Map of the La Jolla district, California. Submarine contours are shown as broken lines. Lat. 32°50' N and long. 117°16'W intersect in La Jolla. The localities described in the text lie between the point *A* in the north and Bird Rock in the south.

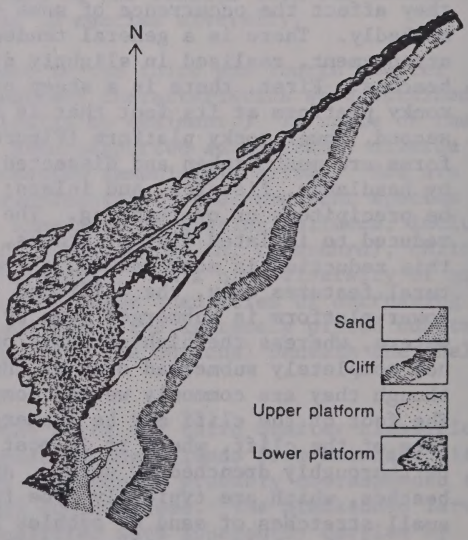


Figure III.C-26

A rocky area at La Jolla, California, showing the typical arrangement of the intertidal rocks in the form of two broken platforms—an upper one and a lower one—below a cliff.

Source: Stephenson and Stephenson, 1972.

The rock colonised by the intertidal organisms is of a curious type. Most of it is sandstone, and of this, the greater part is relatively soft. At its softest, one can rub down the surface of the rock with a fingernail or remove it easily with a knife. But from one small area to another, the consistency varies, and is some places, there are tracts of sandstone that are much harder. In many places, small concretions, boulders, or eminences of hard rock are inset in the softer sandstone, so that it is possible to make a direct comparison of the population of one of the hard insets with that of the surrounding softer rock at the same level. The soft rock, being too friable, forms a poor surface for the attachment of barnacles; but at the same time, it is porous and absorbs sea water, so that it retains moisture in its superficial layers when the tide has receded, which enables lithothamnia to encrust it to levels at which they would otherwise die from desiccation. Conversely, the hard rock, which dries off readily and discourages lithothamnia at such levels, is heavily colonised by barnacles. Apart from the sandstone, there are seams and areas of shale, which also vary in hardness. In some places, the soft shale is riddled by boring bivalves, such as *Petricola californiensis* and *Pholadidea penita*. Conglomerate also occurs locally.

Although many plants and animals prevalent at Pacific Grove occur also at La Jolla, certain southern species, absent or less conspicuous at Pacific Grove, have become important here, and certain northern ones have disappeared. The effects of these changes, taken together with those of the alternation of harder and softer rock and those of the less violent wave action, produce a picture decidedly different from that seen farther north. Here, as at San Francisco, the lowest tides of summer occur in the early morning. Coastal fog is not uncommon at La Jolla, especially in autumn and winter, but is less prevalent than at Pacific Grove.

When examining the biota of a California shore, one must bear in mind that holiday-makers and week-end fishermen frequent many parts of the coast, and that many of them collect, either for food or amusement, various of the plants and animals. Should a shortage of something occur, it is difficult to know whether it is natural or artificial. Collecting of intertidal organisms is very common at La Jolla, but because people's interests are very restricted, it seems to change the general picture very little. Collecting does, however, decidedly reduce the numbers of *Haliotis* at La Jolla.

The Stevensons summarized vertical zonation at La Jolla as follows:

The zonation at La Jolla is normal for a warm-temperate region, except insofar as it is modified by the nature of the rock (Figure III.C-27 and 28). The supralittoral fringe has the usual population of periwinkles, limpets, and high-level isopods. The black zone, discontinuous in some places, is heavily marked in others.

The midlittoral zone is unusually complex. The lower midlittoral is normal--as at Pacific Grove, it is carpeted by a brownish turf of rather small algae, typically with a sharp upper limit. In the upper midlittoral, however, the barnacles are so patchily developed that they are much less conspicuous than they are on most shores; this tends to make the limpets (especially *Acmaea digitalis*) unusually conspicuous. Moreover, there is a belt immediately above the lower midlittoral turf in which, on the soft rock (but not on the hard), a thin crust of lithothamnia was more or less continuous--a very unusual feature. Above this, near the middle of the zone, there is a belt of intermittent lithothamnia.

The infralittoral fringe is populated by a continuation of the algal turf of the lower midlittoral (with a change in the constituent species), among which larger plants (especially *Egregia, Eisenia, Halidrys*, and *Phyllospadix*) are common. This constitutes a laminarian zone, but a weak or shadowy one, compared with that of Pacific Grove or with those of cold-temperate regions in general (Figure III.C-29).

Figure III.C-27

The zonation of the La Jolla region. Areas of hard rock (where *Chthamalus* and *Tetraclita* are abundant and lithothamnia is absent) are included for comparison with the prevalent areas of soft rock.

Source: Stephenson and Stephenson, 1972.

FIGURE III.C-28
The zonation of a rocky area south of La Jolla and a little north of Bird Rock. This figure supplements

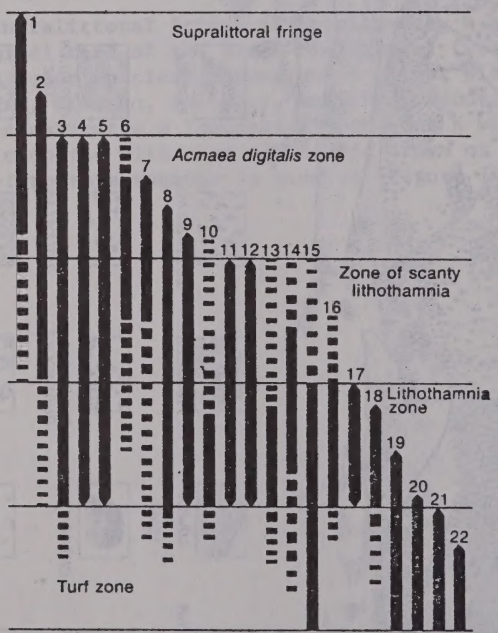


FIGURE III.C-29
The distribution of some common species in relation to the zones in the La Jolla district: 1, *Littorina planaxis;* 2, *Acmaea digitalis;* 3, *Chthamalus;* 4, *Acmaea scabra;* 5, *Acmaea conus;* 6, *Scytosiphon;* 7, *Endocladia;* 8, *Petrospongium;* 9, *Lottia;* 10, *Nuttallina;* 11, *Balanus glandula;* 12, *Pollicipes,* 13, *Tetraclita squamosa rubescens;* 14, *Mytilus;* 15, lithothamnia; 16, *Anthopleura elegantissima;* 17, *Spiroglyphus;* 18, *Acmaea limatula;* 19, *Phragmatopoma;* 20, *Pseudochama;* 21, turf; 22, *Halidrys.* The diagram refers to the La Jolla district in general, though exceptions to it are found in specific areas, especially where the lithothamnia zone is suppressed.

Source: Stephenson and Stephenson, 1972.

D. Bays and Estuaries of Southern California

The majority of this section is taken from Ho (1974) of the Southern California Ocean Studies Consortium, but the bays and marshes of Southern California will first be summarized from Coastal County Fish and Wildlife Resources and Their Utilization (Calif. Dep. Fish and Game {1973}).

Santa Barbara County. Locations of the important wetlands are shown on Figure III.D-1. Table III.D-1 lists amounts of marsh, mud flat, and open water.

Table III.D-1

IMPORTANT WETLANDS OF SANTA BARBARA COUNTY
POSSESSING WILDLIFE HABITATS

AREA	Type of Habitat	Hectares
Santa Maria River	Marsh	20
	Water	6
Santa Ynez River	Marsh	44
	Water	20
Devereux Ranch Lagoon	Marsh	6
	Water	12
Goleta Slough	Marsh	104
Goleta Point Marsh	Marsh	10
	Water	14
El Estero (Carpinteria Marsh)	Marsh	60
	Mud flat	14
	Water	6
TOTAL	Marsh	244[a]
	Mud flat	14[b]
	Water	58[c]

Source: State of California, Department of Fish and Game, 1973.

[a]Percentage of county wetlands: 77.2%

[b]Percentage of county wetlands: 4.4%

[c]Percentage of county wetlands: 18.4%

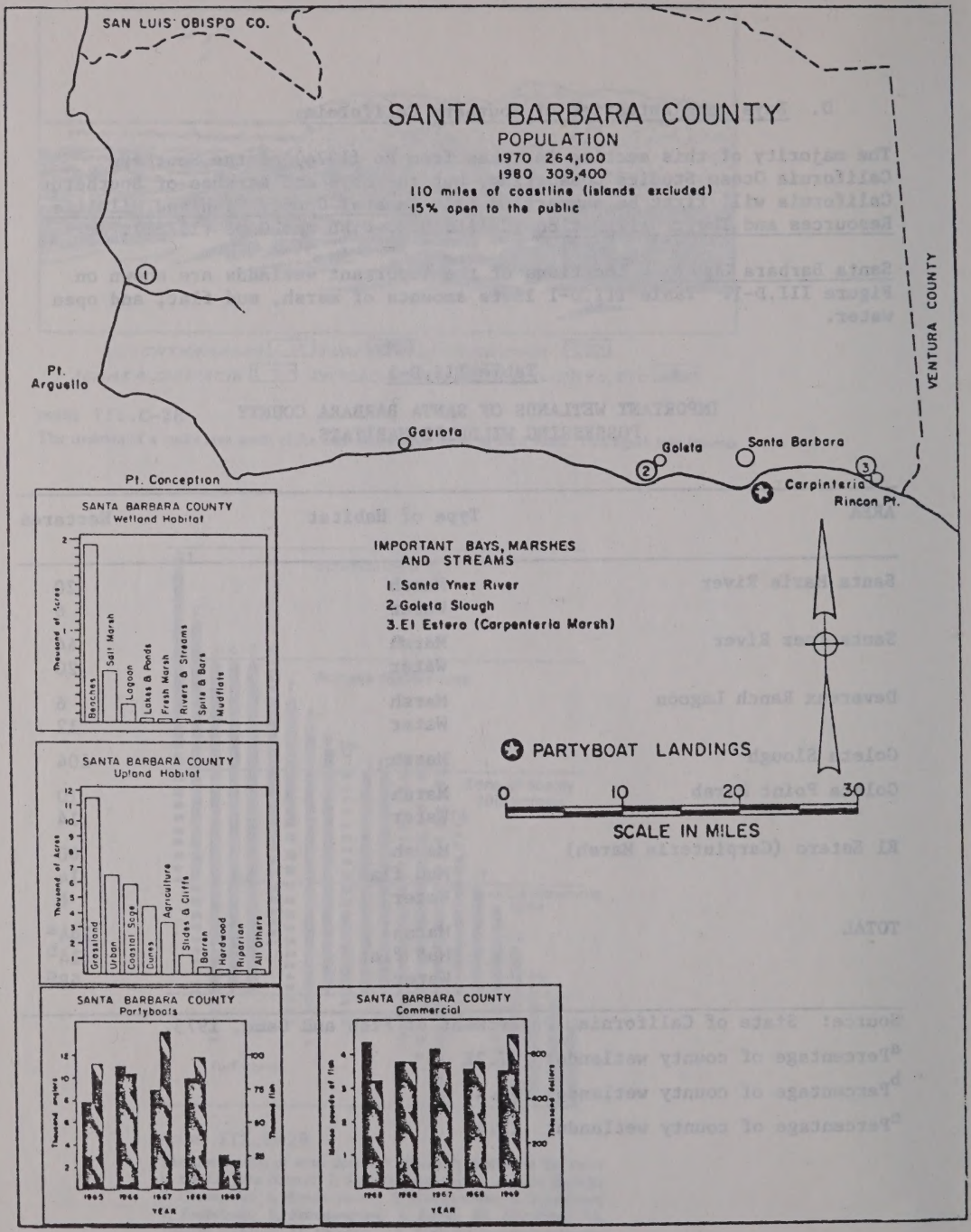


Figure III.D-1. Important wetlands of Santa Barbara County.
Source: State of California, Department of Fish and Game, 1973.

Goleta Slough, Carpinteria Marsh, and the mouth of the Santa Ynez River, comprising 80 percent of the county's wetlands, are of major importance to the maintenance of numerous wildlife species. These marshes appear to be relatively unaltered by human habitation.

Ventura County. Locations of the important wetlands are shown on Figure III.D-2. Amounts of marsh, mud flat, and open water are listed in Table III.D-2.

Table III.D-2

IMPORTANT WETLANDS OF VENTURA COUNTY
POSSESSING WILDLIFE HABITATS

AREA	Type of Habitat	Hectares
Ventura River	Marsh	2
	Water	2
Santa Clara River	Marsh	16
	Water	8
McGrath Lake	Marsh	2
	Water	6
Mugu Lagoon	Marsh	568
	Mud flat	200
	Water	100
TOTAL	Marsh	588[a]
	Mud flat	200[b]
	Water	115[c]

Source: State of California, Department of Fish and Game, 1973.

[a]Percentage of county wetlands: 65%
[b]Percentage of county wetlands: 20%
[c]Percentage of county wetlands: 15%

The wetlands at Mugu Lagoon are considered the most important in the county, comprising some 95 percent of the total. A fish and wildlife plan was prepared jointly by the California Department of Fish and Game and the Bureau of Sport Fisheries and Wildlife for the military installation at Mugu Lagoon. The plan places emphasis on the value of the marsh and provides for its proper management.

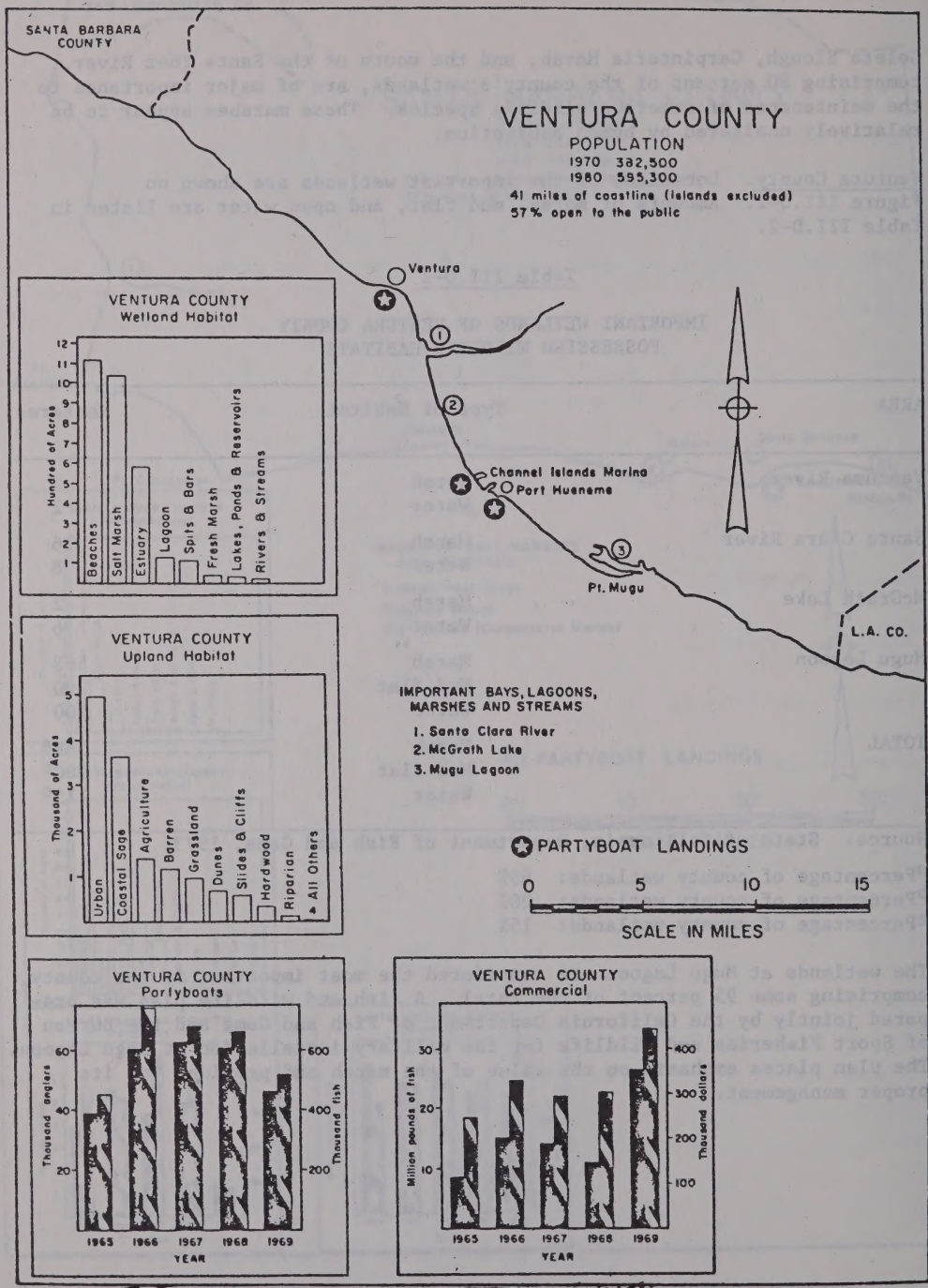


Figure III.D-2. Important wetlands of Ventura County.

Source: State of California, Department of Fish and Game, 1973.

Other county wetlands, while comprising only 5 percent of the total, are extremely important because of the generally arid nature of the adjacent area.

Los Angeles County. The important wetlands are Ballona Creek, Bixby slough, and Colorado Lagoon (Figure III.D-3). Shorebirds, waterfowl, and a number of other water-associated birds are dependent on the county's coastal wetlands for survival. The county possesses some 108 ha (270 acres) of tidal marsh and freshwater marsh, remnants of once large wetland marshes and mud flats. About 96 percent of Los Angeles County's marshes and mud flats have been lost to dredging, filling, and other developments, destroying the value of these habitats for wildlife. The primary value of the remaining marshes is in providing wildlife an oasis of natural habitat in the midst of a metropolis.

Orange County. The locations of the important wetlands are shown on Figure III.D-4, and the amounts of the marsh, mud flat, and open water are presented in Table III.D-3.

The salt marshes, mud flats, and protected waters of Anaheim Bay, Bolsa Bay, and Upper Newport Bay are critical to the maintenance of shorebird and waterfowl populations in the county and State and to support of the Pacific Flyway. These three areas contain almost all of the remaining wetlands in the county.

Anaheim Bay contains about 208 ha (514 acres) of marsh (primarily cordgrass) and mud flats. Under U.S. Navy approval, the California Department of Fish and Game, in cooperation with the U.S. Fish and Wildlife Service, has prepared a Fish and Wildlife Plan for the Seal Beach Naval Weapons Station. The plan identifies the need for maintaining and enhancing the marsh and requires that no enroachments shall be made into the marsh without first exploring all alternatives.

Bolsa Bay has been drastically altered during the last century. Oil operations have generated a network of roads and paths throughout the marsh. Tidegates were installed in the main channel to the bay in the late 1800's. Though the flora and fauna of the bay have been modified, there remains a great potential for restoring the bay's natural capacity to support fish and wildlife species. A restored marsh will provide habitat for the light-footed clapper rail (*Rallus longirostris levipes*) and the California least tern (*Sterna albifrons browni*), both of which are on the U.S. List of Endangered Fauna.

A permanent haven for these birds and hundreds of forms of marine life was assured by a milestone land transaction between the State and Signal Properties, Inc. The agreement signed by Governor Ronald Reagan on March 15, 1973, gave the State fee title to 225.2 ha (556 acres) of land directly

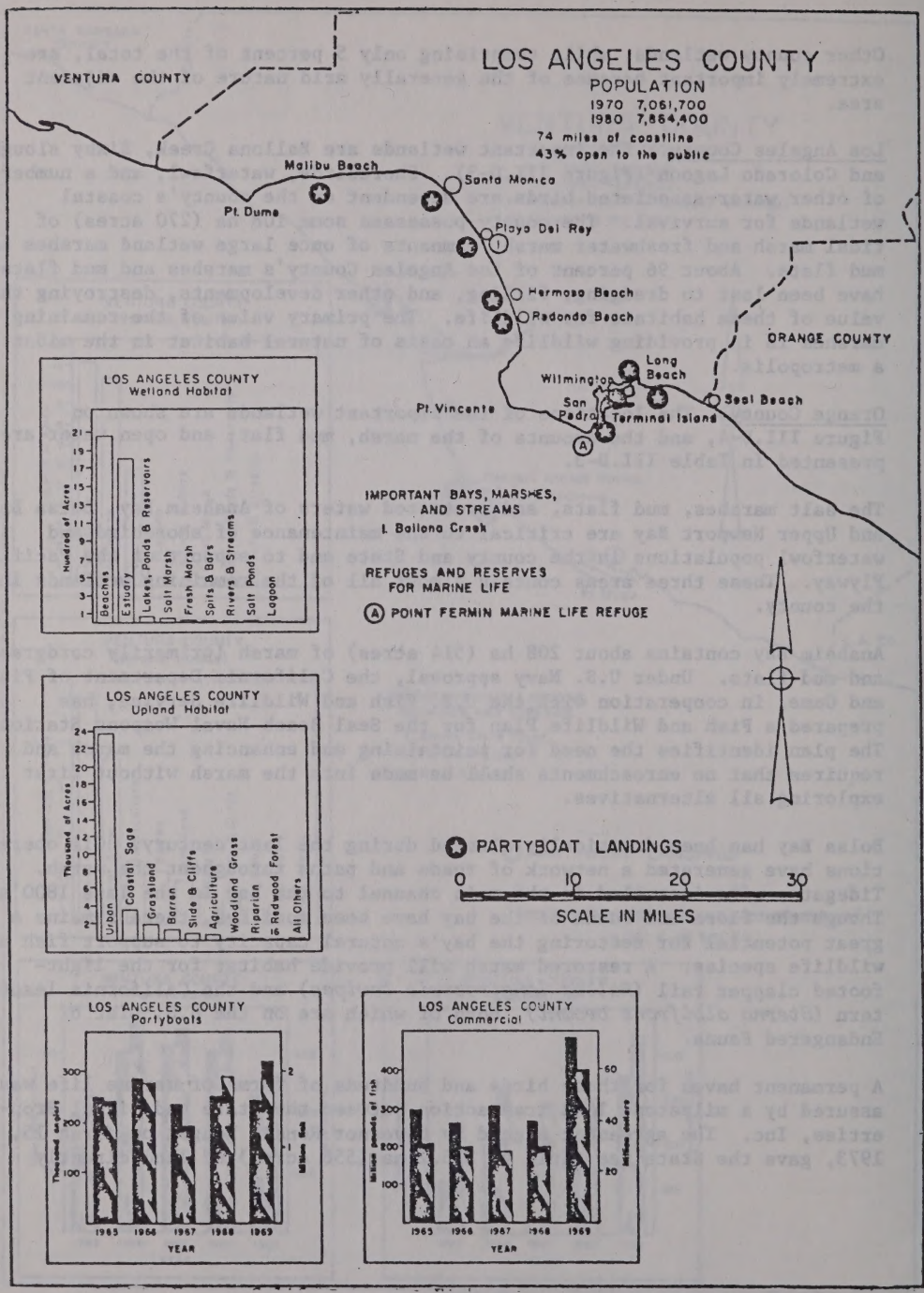


Figure III.D-3. Important wetlands of Los Angeles County.

Source: State of California, Department of Fish and Game, 1973.

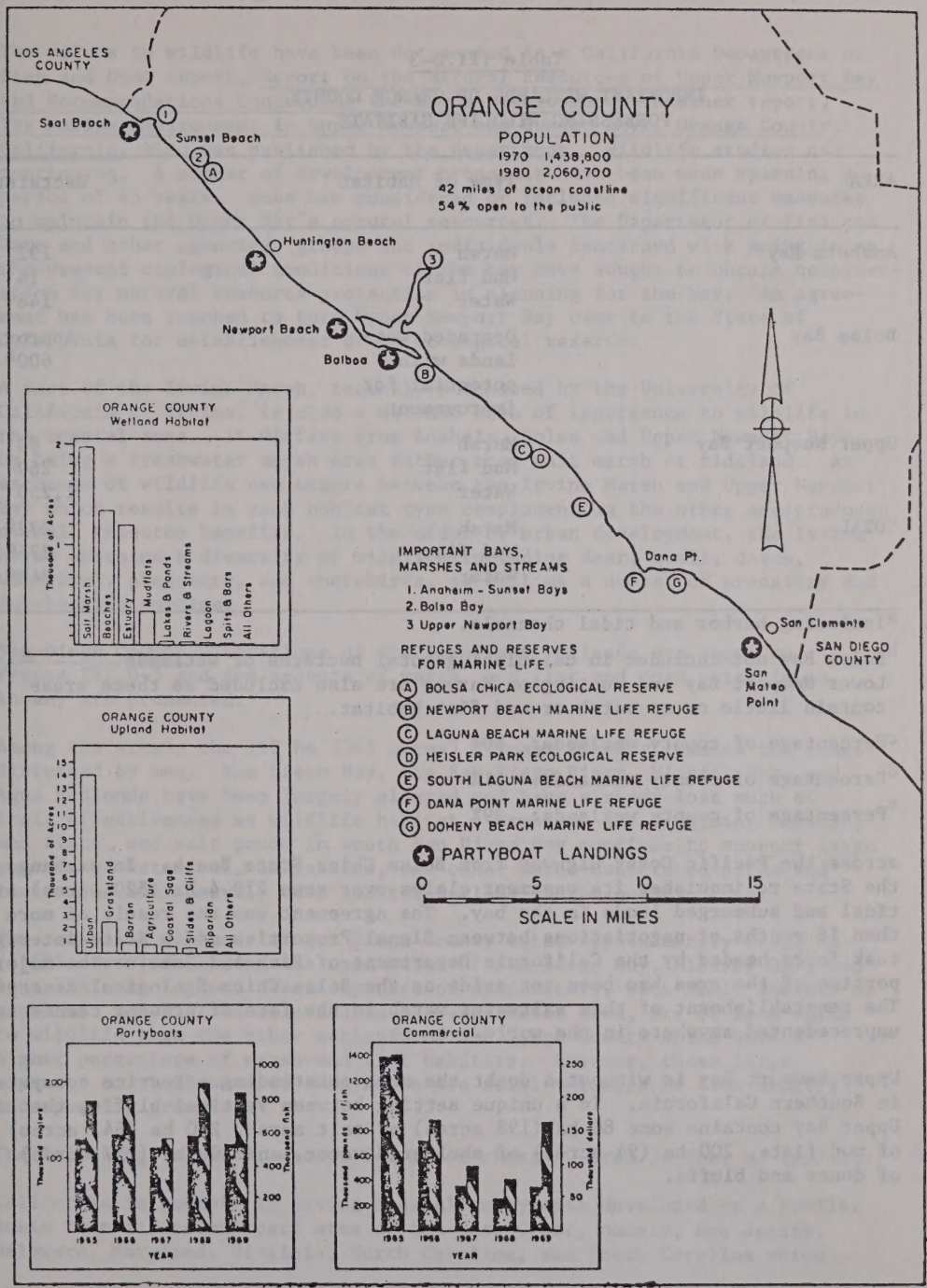


Figure III.D-4. Important wetlands of Orange County.

Source: State of California, Department of Fish and Game, 1973

Table III.D-3

IMPORTANT WETLANDS OF ORANGE COUNTY
POSSESSING WILDLIFE HABITATS

AREA	Type of Habitat	Hectares
Anaheim Bay	Marsh	192
	Mud flat	16
	Water	148[a]
Bolsa Bay	Degraded wetlands with potential for improvement	Approx. 600[b]
Upper Newport Bay	Marsh	80
	Mud flat	260
	Water	1,250
TOTAL	Marsh	272[c]
	Mud flat	276[d]
	Water	348[e]

[a]Including harbor and tidal channels.

[b]Bolsa Bay not included in calculating total hectares of wetlands. Lower Newport Bay and Huntington Harbor are also excluded as these areas contain little or no marsh or mud flat habitat.

[c]Percentage of county wetlands: 30%

[d]Percentage of county wetlands: 31%

[e]Percentage of county wetlands: 39%

across the Pacific Coast Highway from Bolsa Chica State Beach. In exchange, the State relinquished its easement claims over some 210.4 ha (520 acres) of tidal and submerged lands in the bay. The agreement was the result of more than 18 months of negotiations between Signal Properties and a State interagency task force headed by the California Department of Fish and Game. The major portion of the area has been set aside as the Bolsa Chica Ecological Reserve. The reestablishment of this saltwater marsh in the face of present trends is unprecedented anywhere in the world.

Upper Newport Bay is without a doubt the most outstanding estuarine ecosystem in Southern California. In a unique setting between vertical bluffs, the Upper Bay contains some 80 ha (198 acres) of salt marsh, 260 ha (642 acres) of mud flats, 200 ha (94 acres) of sheltered water, and 104 ha (257 acres) of dunes and bluffs.

The values to wildlife have been documented in a California Department of Fish and Game report, Report on the Natural Resources of Upper Newport Bay and Recommendations Concerning the Bay's Development. Another report, The Marine Environment in Upper Newport and Sunset Bays, Orange County, California, also was published by the department. Wildlife studies are continuing. A number of development proposals have been made spanning a period of 45 years. None has considered or included significant measures to maintain the Upper Bay's natural resources. The Department of Fish and Game and other agencies, groups and individuals concerned with maintaining the present ecological conditions of the bay have sought to obtain consideration for natural resource protection in planning for the bay. An agreement has been reached to turn Upper Newport Bay over to the State of California for establishment of an ecological reserve.

A part of the Irvine Marsh, recently purchased by the University of California at Irvine, is also a wetland area of importance to wildlife in the coastal zone. It differs from Anaheim, Bolsa and Upper Newport Bays, by being a freshwater marsh area rather than salt marsh or tideland. An exchange of wildlife use occurs between the Irvine Marsh and Upper Newport Bay which results in each habitat type complementing the other and produces overall resource benefits. In the midst of urban development, the Irvine Marsh contains a diversity of wildlife including deer, quail, doves, waterfowl, pheasants, and shorebirds, as well as a number of predatory and fur-bearing species.

San Diego County. Locations of the important wetlands are shown on Figure III.D-5 and the amounts of marsh, mud flat and open water (when known) are presented.

Among the areas, the 160 ha (395 acres) Tijuana Estuary remains the least disturbed by man. San Diego Bay, the San Diego River, Mission Bay, and Agua Hedionda have been largely altered and have already lost much of their effectiveness as wildlife habitat. However, the remaining marshes, mud flats, and salt ponds in south San Diego Bay continue to support large numbers of waterfowl, shorebirds, and other water-associated birds and remain the most heavily used coastal wetland in the county.

The remaining wetlands of San Diego County total approximately 1,892 ha (4,673 acres) excluding the open water of San Diego Bay, Mission Bay, and Agua Hedionda Lagoon. Vast expanses of open waters, with small amounts of marsh and mud flat in relation to the open water area, are of less value to wildlife than the other wetlands of San Diego County which have a higher percentage of marsh-mud flat habitats. However, these large expanses of shallow-water embayments are still valuable as fish nursery and spawning grounds.

The following is taken, except for minor changes, from Ju-Shey Ho (1974).

California is notable in having coastal embayments developed on a smaller scale than its counterpart area of the East Coast, namely, New Jersey, Delaware, Maryland, Virginia, North Carolina, and South Carolina which

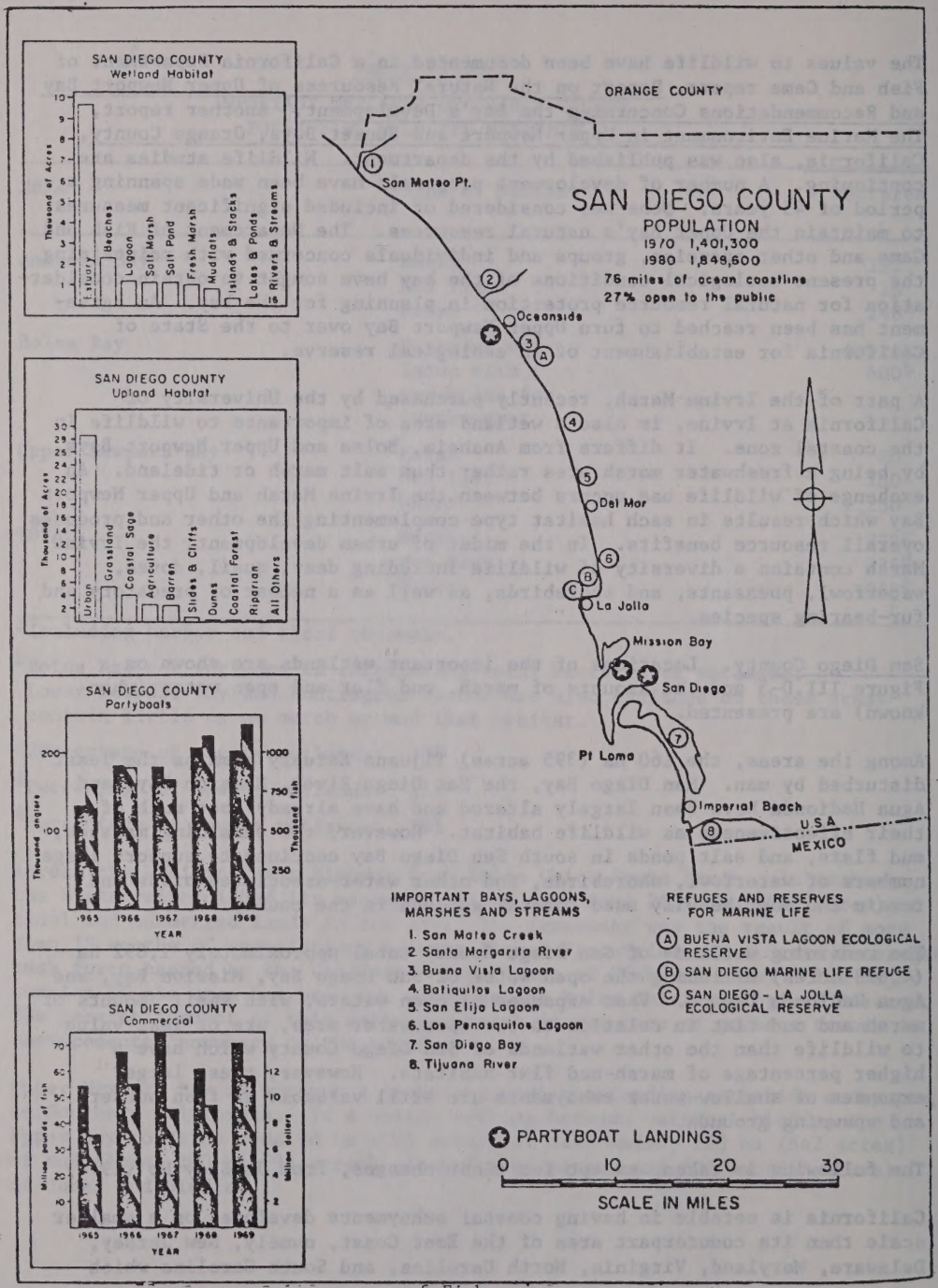


Figure III.D-5. Important wetlands of San Diego County.

Source: State of California, Department of Fish and Game, 1973.

Table III.D-4

IMPORTANT WETLANDS OF SAN DIEGO COUNTY
POSSESSING WILDLIFE HABITATS

AREA	Type of Habitat	Hectares
San Mateo Creek	Wetlands (undifferentiated)	70
Santa Margarita Lagoon	Wetlands (undifferentiated)	240
Buena Vista Lagoon	Wetlands (undifferentiated)	12
Agua Hedionda Lagoon	Wetlands (undifferentiated but primarily water)	120
Batiquitos Lagoon	Wetlands (undifferentiated)	240
San Elijo Lagoon	Wetlands (undifferentiated)	200
Los Penaquitos Lagoon	Wetlands (undifferentiated)	4
San Diego River	Wetlands (undifferentiated)	100[a]
Mission Bay	Marsh	8
	Water	936
San Diego Bay	Marsh	144
	Mud flat	240
	Water	4,840
	Salt ponds	560
Tijuana River	Wetlands (undifferentiated)	160
TOTAL	Wetlands (excluding the acreage of bay waters in San Diego and Mission Bays and Agua Hedionda Lagoon	1,978

[a]Includes 150 acres of eelgrass.

stretch their total coastline almost in the same latitudinal range as California. This is particularly true of the coast of Southern California, where, because of arid climate and rather recent geological setting, there is no large river entering the sea. Consequently, the bays on the coast of Southern California are necessarily small, with the largest one, San Diego Bay, only 48.24 km^2 (18.8 square miles) at mean low water (Anonymous, 1950). Furthermore, the absence of a coastal plain in Southern California has restricted the development of salt marsh to small areas fringing sheltered bays and lagoons.

The bays considered here are those tracts of water extending into the land and remaining connected to the sea only by a restricted, narrow entrance. Rivers in Southern California are seasonal streams and in their natural state are sealed off at their mouths by beach deposits during the dry seasons. Most of the so-called "bays" are actually submerged mouths of the major streams, such as San Pedro Bay, Upper Newport Bay, and Anaheim Bay, or separated from the sea by spits and tombolos, such as Lower Newport Bay, Mission Bay, and San Diego Bay. All of these characteristics are products of the strong surf along the exposed Pacific shore (Gasline, 1967). Some other bodies of water that are loosely termed bays, such as Santa Monica and La Jolla Bays, which are neither landlocked embayments nor derivatives of an estuary with salt marsh development, are, accordingly, not considered.

Several small lagoons in San Diego County are not periodically flushed by the tide (Table (A)F.1-1 in Appendix F.1). One of them, the Buena Vista Lagoon, has been completely separated from the sea for so many years that its salinity (3.0-6.5°/$_{oo}$) is much lower than other embayments of Southern California. Consequently, its fauna and flora are mixed with some freshwater types (Carpelan, 1964). All other embayments have a mean salinity of about 32.5°/$_{oo}$.

Salt marshes are tracts of land in the bays, estuaries, or lagoons that are covered with halophytes and subject to periodic flooding by the tide. The striking feature of the marsh environment is the great variation in values of the parameters known to affect the occurrence and development of animal population. In the marsh of Mission Bay, for instance, Phleger and Bradshaw (1966) have recorded considerable diurnal and seasonal variation in pH, oxygen, water temperature, and salinity. These variances are related to tidal flushing, air temperature variation, sunlight duration, and marsh plant metabolism.

The great influx of residents to Southern California during and following World War II, resulted in substantial alteration of the natural state of the southland; nearly all of the bays and lagoons have been modified by the activities of man through construction of marinas and breakwaters, building of roads and railroads, dredging of channels, diversion of rivers, and use for waste disposal. Of the existing embayments Mugu Lagoon, Upper Newport Bay, and Tijuana Estuary are some of the major embayments that still remain in a relatively unaltered condition. (Figures III.D-6 and 7). The California Coastal Zone Conservation Commission (1975) policy for estuaries and wetlands states that "all remaining coastal estuaries and wetlands and buffer areas necessary to protect wetlands and their wildlife and bird habitat values shall be preserved, enhanced, and where possible, restored." Further restoration of the relatively unaltered Upper Newport Bay and restoration of Bolsa Chica are given high priority.

Estuaries and lagoons support animals recruited principally from the sea. Many neritic animal species use these areas as a nursery ground before migrating to the open sea (Vernberg and Vernberg, 1972). For example, shallow-water fishes such as the California halibut, the Pacific staghorn sculpin, the deepbody anchovy, and the gray smoothhound are known to use Anaheim Bay as nursery habitats. Some permanent dwellers of Anaheim Bay that complete their life cycle in the bay are the topsmelt, the California killifish, the arrow goby, and the diamond turbot.

However, with a profound alteration of coastal wetlands in Southern California, to what extent they still serve as a nursery and feeding ground for neritic animals has not been determined. It is known that the fully developed commercial and residential marina-complex in Mission Bay has destroyed most, if not all, wildlife values there (Speth, 1969). Studies on the benthic animals of Anaheim Bay by Kawuling and Reish (1975) have demonstrated that the density of benthic polychaetes showed striking differences between the dredged and the undredged areas.

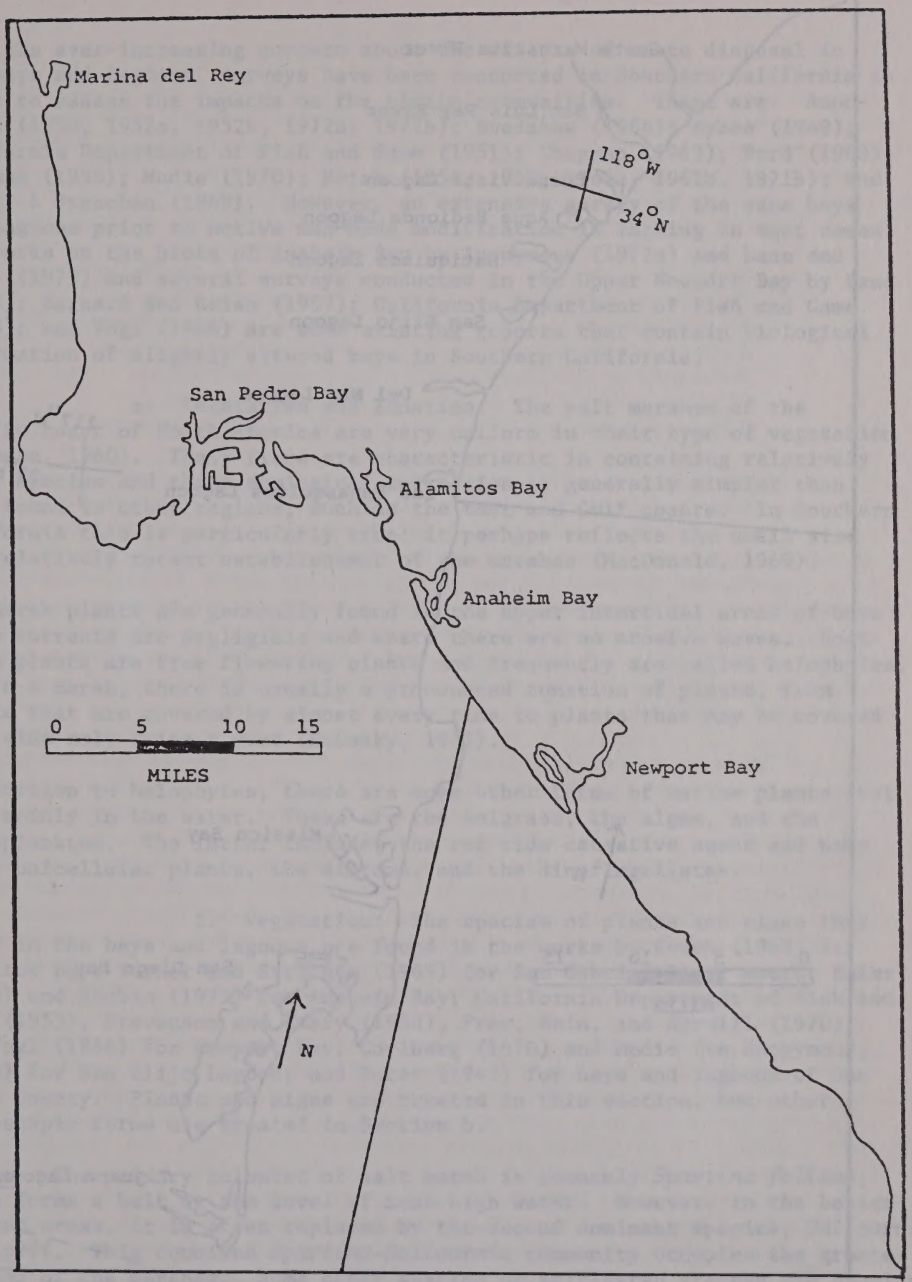


Figure III.D-6. Bays located in Los Angeles and Orange Counties. Source: Ho (1974).

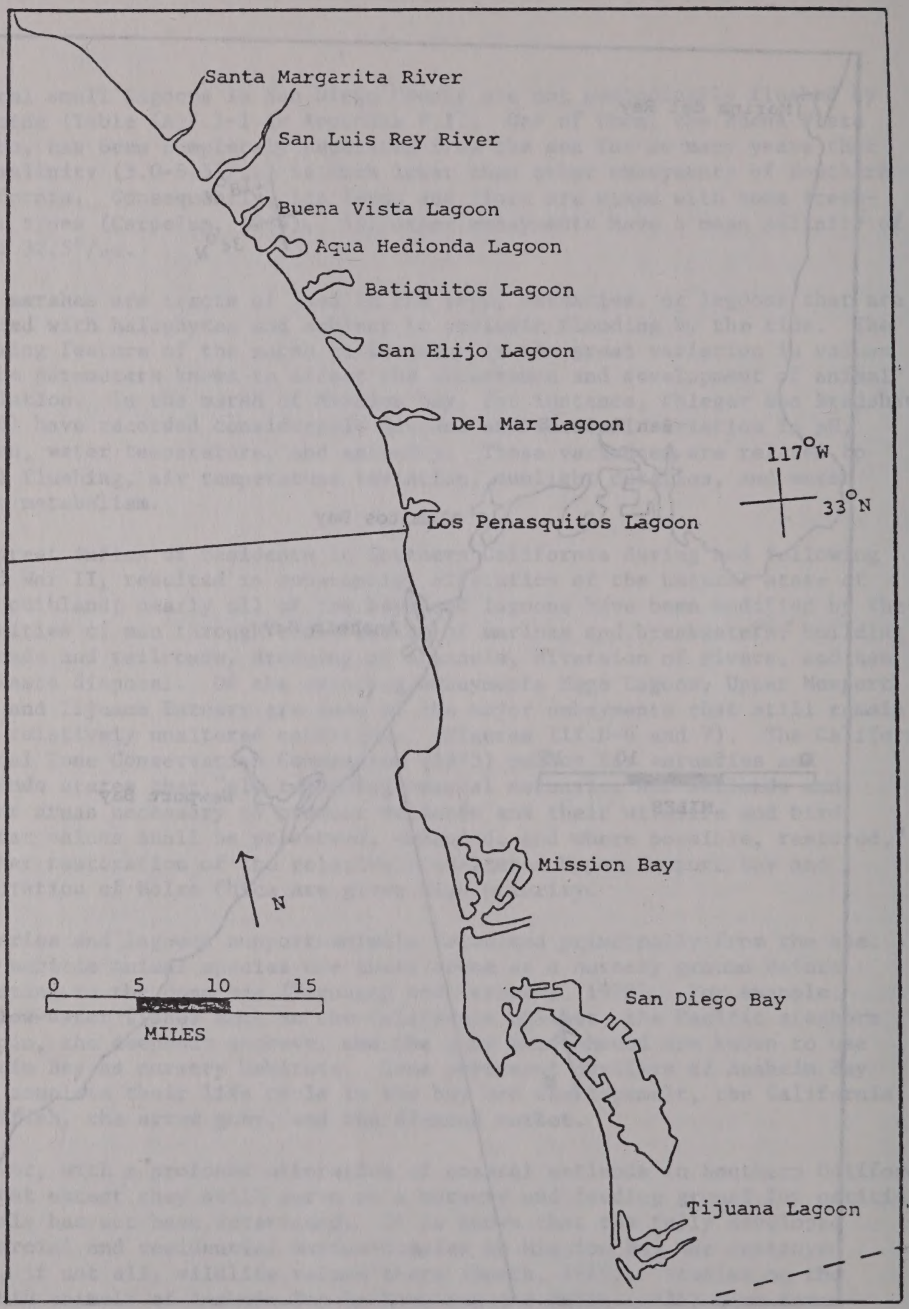


Figure III.D-7. Bays located in San Diego County.
Source: Ho (1974).

With the ever-increasing concern about the effects of waste disposal in the bays and lagoons, surveys have been conducted in Southern California in order to assess the impacts on the biotic communities. These are: Anonymous (1950, 1952a, 1952b, 1972a, 1972b); Bradshaw (1968); Bybee (1969); California Department of Fish and Game (1951); Chapman (1963); Ford (1968); Hartman (1956); Mudie (1970); Reish (1954, 1959, 1961a, 1961b, 1971b); and Turner & Strachan (1969). However, an extensive survey of the same bays and lagoons prior to active man-made modification is lacking in most cases. The works on the biota of Anaheim Bay by Anonymous (1972a) and Lane and Hill (1975) and several surveys conducted in the Upper Newport Bay by Bane (1968); Barnard and Reish (1957); California Department of Fish and Game (1958); and Vogl (1966) are some existing reports that contain biological information of slightly altered bays in Southern California.

a. Vegetation and Zonation: The salt marshes of the Pacific coast of North America are very uniform in their type of vegetation (Chapman, 1960). Their flora are characteristic in containing relatively fewer species and their ecological succession is generally simpler than that found in other regions, such as the East and Gulf coasts. In Southern California this is particularly true; it perhaps reflects the small size and relatively recent establishment of the marshes (MacDonald, 1969).

The marsh plants are generally found in the upper intertidal areas of bays where currents are negligible and where there are no erosive waves. Most marsh plants are true flowering plants and frequently are called halophytes. Within a marsh, there is usually a pronounced zonation of plants, from plants that are covered by almost every tide to plants that may be covered by a tide only twice a year (McLusky, 1971).

In addition to halophytes, there are some other forms of marine plants that grow mainly in the water. These are the eelgrass, the algae, and the phytoplankton. The latter includes the red tide causative agent and many other unicellular plants, the diatoms, and the dinoflagellates.

i. Vegetation: The species of plants and algae that occur in the bays and lagoons are found in the works by Reish (1968) for Alamitos Bay; Turner and Strachan (1969) for San Gabriel River mouth; Baker (1975) and Shubin (1975) for Anaheim Bay; California Department of Fish and Game (1953), Stevenson and Emery (1958), Frey, Hein, and Spruill (1970), and Vogl (1966) for Newport Bay; Carlberg (1970) and Mudie (in Anonymous, 1972b) for San Elijo Lagoon; and Purer (1942) for bays and lagoons of San Diego County. Plants and algae are treated in this section, but other microscopic forms are treated in Section b.

Plants. The primary colonist of salt marsh is commonly *Spartina foliosa*, which forms a belt at the level of mean high water. However, in the better-drained areas, it is often replaced by the second dominant species, *Salicornia bigelovii*. This combined *Spartina-Salicornia* community occupies the greater portion of the marshes. Some other species of salt-marsh grasses are usually

found in association with them. MacDonald (1969) identified seven most frequent associates and discovered that the components of the associate floral groups were quite different north and south of Point Conception. The seven associate species in the two regions are (listed in order of decreasing abundance):

North of Point Conception:	South of Point Conception:
Distichlis spicata	*Frankenia grandifolia*
Triglochin maritima	*Suaeda californica*
Jaumea carnosa	*Monanthochloe littoralis*
Limonium commune	*Triglochin maritima*
Frankenia grandiflora	*Limonium commune*
Glaux maritima	*Jaumea caronosa*
Plantago maritima	*Distichlis spicata*

A comparison of the above lists reveals that south of Point Conception, *Glaux maritima* and *Plantago maritima* were replaced by *Monanthochloe littoralis*, and *Suaeda californica*, although abundance values were not comparable; the most abundant species of the north, *Distichlis spicata*, became the least abundant in the south; and the fifth abundant species in the north, *Frankenia grandifolia*, rose to the most abundant species of the south. It should be mentioned that in his ecological study of the plants of the 12 marshlands of San Diego County, Purer (1942) found that *Atriplex watsonii* and *Batis maritima* were much more abundant that *Triglochin maritima* and *Jaumea caronosa*.

Algae. The most common and abundant algae is the tubular, filatemtous form of green seaweed, *Enteromorpha crinita*. This species can withstand a wide range of salinity, temperature, and exposure to air and therefore is the most widely distributed algae occurring in bays and lagoons, particularly in quiet-water areas. Another factor contributing to the ubiquity and abundance of *Enteromorpha* in San Diego County is, assumed by Bradshaw and Mudie (1972), the discharge of nutrient-rich sewage effluent into the lagoons. On the mudbanks of quieter water in Anaheim Bay, this species of green algae was reported to form a mat covering an area as large as 7 m^2 (8.4 square yards) with 5 cm (2 inches) thickness (Shubin, 1975).

In contrast to the salt-marsh grasses which are virtually eliminated from substantially altered bays, the species of flat, sheet-like green algal genus, *Ulva*, are very common in harbors and marinas, growing on rocks or attaching to boat floats. It is particularly abundant in the spring and fall months. It is interesting to note that while *Ulva* spp. are abundant in the substantially modified Alamitos Bay (Reish, 1968), they are the least abundant species of all the algae surveyed in the rather unaltered Anaheim Bay (Shubin, 1975). The brown algae seems to be the least abundant of the three algal groups to occur in bays or harbors (see Table III.D-5).

Table III.D-5

NUMBER OF ALGAL SPECIES OCCURRING
IN SOUTHERN CALIFORNIA EMBAYMENTS

LOCALITY	Green algae (Chlorophyta)	Brown algae (Phaeophyta)	Red algae (Rhodophyta)	Total
Alamitos Bay	3	5	9	17
San Gabriel River Mouth	3	1	15	19
Anaheim Bay	11	-	2	13
Newport Bay	5	4	11	20

Source: compiled from Reish, 1968; Turner & Strachan, 1969; Frey, Hein and Spruill, 1970.

In Purer's (1942) work on the flora of marshlands in San Diego County, not a single species of brown algae was reported. The three out of four species of brown algae reported from Upper Newport Bay (Frey, Hein, and Spruill, 1970) were listed as rare, with their occurrence being less than 4.9 percent of the flora. Of the 16 species of brown algae listed in The Marine Life of Southern California (Reish, 1972), only three species: *Colpomenia sinuosa*, *Ectocarpus confervoides*, and *Hydroclathurus clathratus*, were mentioned to have been found in the bays or harbors. The poor occurrence of brown algae is another characteristic of the Southern California marshes and bays.

ii. Zonation: The zonation of plants in salt marshes is generally governed by the operation of the following environmental factors: tides, water table, soil structure, water movement, aerated layer, soil salinity, soil moisture, and biota (Chapman, 1964). However, it seems that tide is the single, most important factor in determining the distribution of salt marsh plants (McLusky, 1971). According to Ranwell (1972), the tidal factors of particular importance include: the mechanical disturbance (which controls intensity and frequency of sedimentation and erosion); the vertical range (which controls tidal flooding depths and the vertical extent of salt marsh); the form of tidal cycle (which controls frequency and duration of submergence and emergence); and the water quality (which controls the amount of light reaching submerged growths and the salinity).

Both Chapman (1960) and MacDonald (1969) have noted that above the level of MLHW (mean low high water; the intertidal zone that is exposed at least once every 24 hours) there are two major subenvironments in a marsh, namely, the low marsh and the high marsh (Figure III.D-8). The former extends from the lower limit of salt marsh vegetation to the level of MHHW

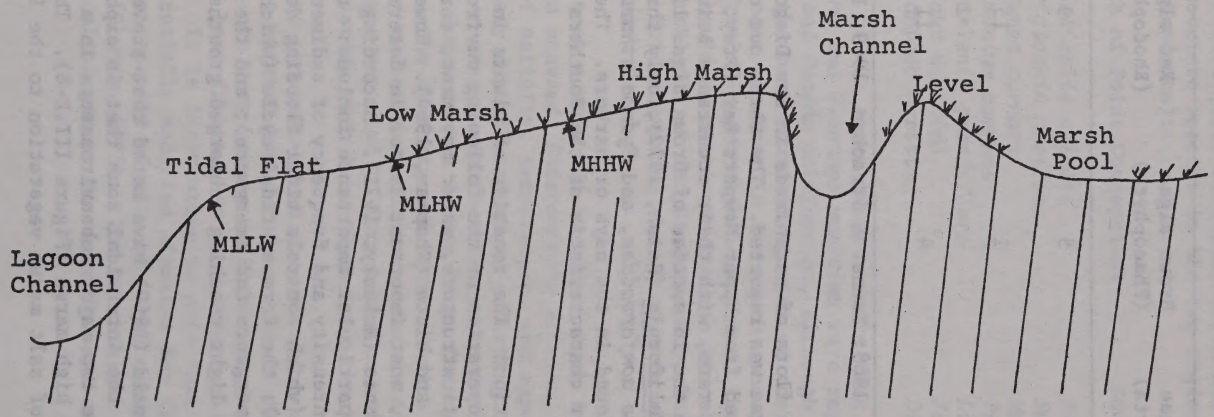


Figure III.D-8. Diagrammatic cross-section of tide levels and marsh zones in Mission Bay (after Phleger, 1970).

Source: Ho (1974).

(mean high high water; with more than 6 hours of tidal submergence at each tide and less than 15 days of continuous tidal emergence), and the latter includes the zones between the levels of MHHW and EHW (extreme high water; with less than 6 hours of tidal submergence and may be exposed in the air for several weeks or even months). Thus, the major difference between the two subenvironments is the frequency and the duration of emergence and submergence. The area between MLHW and MLLW (mean low low water) is called tidal flat, and the land there is submerged in water most of the time, except during extremely low tides.

The rate of supply of gaseous carbon dioxide (CO_2) for photosynthesis is severely limited during submergence, and different species may differ in their sensitivity to such limitation. Also, the lower regions of a salt marsh are covered by almost every tide, and the soil will often be water-logged; whereas plants in the upper regions are more rarely covered, and the soil will have more opportunity for drainage. Therefore, a gradient in the sensitivity to CO_2 limitation and in the ability to live in water-logged soils may be the important factor in determining marsh plant zonation (McLusky, 1971).

The eelgrass, *Zostera marina*, is the most common angiosperm growing on the permanently inundated marshlands. This lowest vegetative zone is called the Zosteretum. In relatively unaltered bays, such as Anaheim and Upper Newport bays, the eelgrass is usually widespread. However, in substantially altered bays, such as Mission or San Diego Bays, it is reduced to small patches; and in Alamitos Bay and San Pedro Bay, this species has disappeared because of dredging operations and other activities of man.

Above the Zosteretum, in Upper Newport Bay, Stevenson and Emery (1958) identified five additional zones: Spartinetum, Salicornietum, Suaedetum, Monanthocloetum, and Distichlidetum. Each zone was named after the dominant species that occurred in it: *Spartina foliosa* (cordgrass), *Salicornia bigelovii* (pickleweed), *Suaeda californica* (seablite), *Monanthochloe littoralis* (shoregrass), and *Distichlis spicater* (saltgrass). However, in Anaheim Bay, Baker (1975) could identify only three additional zones: Spartinetum, Batietum/ Salicornietum, and Distichlidetum.

It is noted that in San Elijo Lagoon (Anonymous, 1972b) and other periodically closed small lagoons in San Diego County, the typical salt marsh grasses, e.g., cordgrass, pickleweed, arrowgrass, *Triglochin maritima*; saltwort, *Batis maritima*; and eelgrass, of the permanently submerged zones in Southern California are absent. This absence is apparently associated with the absence of continuous tidal flushing in these lagoons. Furthermore, because of the lack of frequent tidal action, the characteristic vertical zonation of salt marsh vegetation is weakly developed in San Elijo Lagoon. In Mission Bay, the *Spartina* community occupies about 60 percent of the marsh area.

It occurs from about +1.0 to +1.5 m (3.3 to 4.9 feet) above the elevation of mean low low water. At +1.5 to +1.8 m (4.9 to 5.9 feet) an area of about 1.4 percent of the marsh, the flora is dominated by *Salicornia* and *Batis*. Above this level there is a community characterized by *Suaeda* and it takes up about 23 percent of the marsh area (Phleger, 1970).

b. Plankton Community: Although many studies and surveys have been made on the benthic life of bays and lagoons, only a few works have been carried out on the planktonic life of the same water bodies. Furthermore, most of the works were made in the form of unpublished theses and reports and confined to three bays: Anaheim Bay (Felts, 1973; Howey, 1971; Slawson, 1972; Sowby, 1973); Mission Bay (Fairbanks, 1969; Snyder, 1965); and San Diego Bay (Damon, 1969; Sweeney and Clendenning, 1958). Certainly, this biotic community in the Southern California bays and lagoons deserves much more attention than it has received.

Estuaries and bays, with their semienclosed nature, permit the maintenance of a plankton community that is at least native, if not strictly endemic (Riley, 1967). A survey of microbiota by Lackey (1967) reported 57 species of dinoflagellates and 41 species of ciliates from San Diego Bay, and 49 species of dinoflagellates and 23 species of ciliates from Mission Bay, but only 25 species of the former and four species of the latter were common in both bays, in spite of the entrances of the two bays being only about 11.2 km (6.9 miles) apart. The environmental factors controlling this specific feature of "native" population in estuarine plankton community are: degree of bay enclosure, shape of basin, temperature, salinity, water circulation, and cycling rate of elements. Riley explained that the maintenance of native population in an estuary and, conversely, the rate of invasion by coastal water forms will depend in part on the flushing rate and circulation pattern. From a dynamic standpoint, obviously, the rate of increase of the population must balance the rate of loss by flushing, predation, and all other natural causes in order for the population to maintain itself. In general, it is more of a problem for zooplankton than for phytoplankton.

Another characteristic feature of the plankton community in estuaries and bays is its large volume but small number of species. As in Anaheim Bay, the annual mean plankton volume was 0.451 ml/m^3, which is about two to six times more than has been previously reported for plankton volumes for the waters off the Southern California coast (Howey, 1971). However, of the 12 species of copepods that occurred in the bay, one species, *Acartia tonsa*, comprised an average of 89.6 percent of all copepods throughout the year.

i. Phytoplankton: The phytoplankton comprise all photosynthetic planktons. They are usually microscopic and composed of either a single cell or chains of loosely bound cells. Reproduction in phytoplankton is accomplished chiefly by binary fission in which each cell divides to produce two daughter cells. This population increase by geometric progression is of great ecological importance, since it

enables a rapid response to favorable growing conditions and in certain circumstances may result in a bloom. An extensive bloom of the dinoflagellate *Gonyaulax polyhedra* occurred in Alamitos Bay in mid-September through mid-November, 1962, and was reported by Reish (1963) to be responsible for elimination of 26 various species of benthic polychaetes, crustaceans, and mollusks.

Composition of Phytoplankton. Diatoms and dinoflagellates are the two major groups of phytoplankton. A total of 26 genera of diatoms (Bacillariophyta) and 20 genera of dinoflagellates (Pyrrophyta) were reported by Fairbanks (1969) and Lackey and Clendenning (1965) from Mission and San Diego Bays, respectively. However, only ten genera of diatoms (*Thalassionema, Chaetoceros, Thalassiosire, Asterionella, Skeletonema, Coscinodiscus, Nitzschia, Navicula, Thalassiothrix*, and *Grammatophora*) and five genera of dinoflagellates (*Dinophysis, Prorocentrum, Peridinium, Ceratium*, and *Gonyaulax*) were recorded as major plankton, i.e., occurring in numbers larger than 5 percent of the total phytoplankton at least once a year. Lackey and Clendenning (1965) noticed that while populations of other phytoplankton were larger at the inner part of San Diego Bay than at the coastal areas, the opposite was true of the dinoflagellates.

In addition to diatoms and dinoflagellates, the phytoplankton of coastal embayments also consists of Volvocales, Chlorphyta, Euglenophyta, Cryptophyta, and Chrysophyta. The Volvocales are relatively common to inshore waters and are fairly well represented with nine species occurring in San Diego Bay. Plankton Chlorococcales (Chlorphyta) are not regarded as common in marine waters. However, in San Diego Bay, 26 blooms (500 cells/ml) were recorded from July 6 to August 9, 1959. The colorless Euglenophyta are far more common and often more abundant in estuarine waters than the green ones, but the majority of them are benthos, and even those occurring in the plankton are known from the benthic community. Of the 34 species of colorless Euglenophyta in San Diego Bay, only nine species had ever been collected in water samples. *Eureptia* is a widespread and well recognized marine green euglenoid genus. In San Diego Bay, it is represented by *E. lanowii*, which produced only one bloom in the summer of 1959. Cryptophyta seem to be the most ubiquitous of all plankters. There are perhaps five genera (*Chilomonas, Chromonas, Cryptomonas, Cyathomonas*, and *Rhodomonas*) which appear to be important in the ecology of estuarine waters. All five genera are found in San Diego Bay, and 12 blooms were recorded in 1959. Although 23 species of Chrysophyta were identified from San Diego Bay, only five of them were responsible for the nine blooms observed in the summer of 1959 (Lackey, 1967; Lackey and Clendenning, 1965).

Factors Controlling Phytoplankton Population. The abundance of phytoplankton in the water is generally governed by the amounts of available PO_4 and NO_3. A favorable nitrate/phosphate (N/P) ratio is somewhere between 10:1 and 30:1 as far as abundance is concerned (Lackey, 1976). In Mission Bay, prior to the occurrence of red tide in May, 1968, the N/P ratio was 14.8:1 but dropped to 0.0038:1 when the bloom dissipated (Fairbanks, 1969).

Ryther and Dunstan (1971b) have demonstrated that nitrogen is the critical limiting factor of phytoplankton growth and eutrophication in coastal waters. They also found that about twice as much phosphate as could be used by the phytoplankton and other algae was normally present in the New York Bight. A similar conclusion was reached by Bradshaw and Mudie (1972) in their studies on some aspects of pollution in the bays and lagoons of San Diego County. They provided evidence that a dramatic inorganic nitrogen depletion may occur within a few thousand feet when the effluent enters a shallow, sluggish stretch of lagoon. Apparently, the nitrogen was quickly absorbed by the phytoplankton and other plants. However, phosphate appears to remain in excess of phytoplankton demands.

The red tide of May, 1968, in Mission Bay was closely watched by Fairbanks (1969). Initially, it was produced by the converging mechanism of cold, dense, nutrient-rich bottom water and a steep, shallow thermocline. At the peak of the bloom, cell counts of *Ceratium* reached 7.9×10^6 per liter and were accompanied by high silicate (26.1 mg-at/l) and phosphate (1.5 mg-at/l) concentrations. Nitrate was high at beginning of the bloom (8.9 mg-at/l) and was nearly exhausted by the end (0.01 mg-at/l). Dissipation of the bloom was attributed by him to be the combination of nitrate depletion, grazing by zooplankton (*Noctiluca*, tintinnids, and rotifers) and breaking up of the thermocline. The dinoflagellates associated with this red tide were: *Ceratium*, *Gonyaulax*, *Prorocentrum micans*, and *Peridinium*.

Fairbanks also found that the physical factors appeared to be of more importance to phytoplankton growth in surface waters, whereas nutrient concentration increased in importance with depth. High water temperature, high incident solar radiation, and high salinities appear to be detrimental to phytoplankton growth, especially when coupled with nutrient depletion. Tidal action was found to offset population size at the surface where outgoing water causes the greatest changes, but at the 6-m (19.7 feet) depth the incoming rather than the outgoing tide is of most importance.

Seasonal Fluctuation of Phytoplankton Population. In Mission Bay, the annual phytoplankton cycle was characterized by a major bloom occurring in April and May. During the rest of the year, the population remained fairly constant with the smallest occurring in September in deeper water and January at surface water. However, when diatoms and dinoflagellates are examined separately, a different picture emerges. The diatom cycle appeared very similar to the total phytoplankton cycle, except with less pronounced April-May peaking (Figure III.D-9). The dinoflagellate cycle, however, reached two peaks during the year, as can be seen in Figure III.D-9, one in the fall and another greater one in the spring.

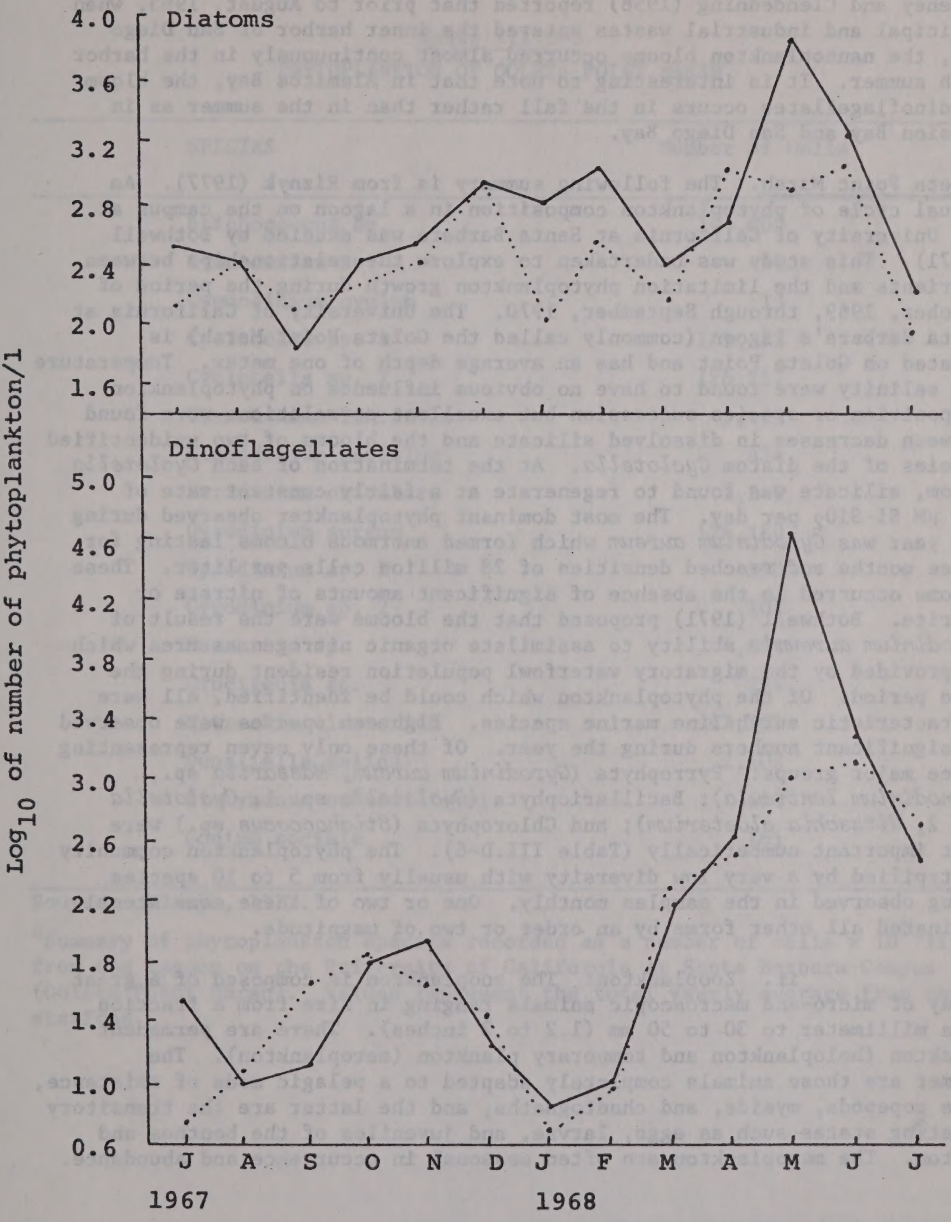


Figure III.D-9. Seasonal abundance of phytoplankton in Quivira Basin, Mission Bay; . . . . . at 0.5-meter depth, at 6-meter depth (after Fairbanks, 1969).

Source: Ho (1974).

Sweeney and Clendenning (1958) reported that prior to August, 1963, when municipal and industrial wastes entered the inner harbor of San Diego Bay, the nannoplankton blooms occurred almost continuously in the harbor each summer. It is interesting to note that in Alamitos Bay, the bloom of dinoflagellates occurs in the fall rather than in the summer as in Mission Bay and San Diego Bay.

Goleta Point Marsh. The following summary is from Riznyk (1977). An annual cycle of phytoplankton composition in a lagoon on the campus at the University of California at Santa Barbara was studied by Bothwell (1971). This study was undertaken to explore the relationships between nutrients and the limitation phytoplankton growth during the period of October, 1969, through September, 1970. The University of California at Santa Barbara's lagoon (commonly called the Goleta Point Marsh) is located on Goleta Point and has an average depth of one meter. Temperature and salinity were found to have no obvious influence on phytoplankton composition or species succession but excellent correlations were found between decreases in dissolved silicate and the blooms of two unidentified species of the diatom *Cyclotella*. At the termination of each *Cyclotella* bloom, silicate was found to regenerate at a fairly constant rate of 3.0 μM $Si-SiO_2$ per day. The most dominant phytoplankter observed during the year was *Gyrodinium aureum* which formed enormous blooms lasting for three months and reached densities of 28 million cells per liter. These blooms occurred in the absence of significant amounts of nitrate or nitrite. Bothwell (1971) proposed that the blooms were the result of *Gyrodinium aureum's* ability to assimilate organic nitrogen as urea which is provided by the migratory waterfowl population resident during the same period. Of the phytoplankton which could be identified, all were characteristic euryhaline marine species. Eighteen species were observed in significant numbers during the year. Of these only seven representing three major groups: Pyrrophyta (*Gyrodinium aureum, Massarita* sp., *Glenodinium lenticula*); Bacillariophyta (*Cyclotella* sp. 1, *Cyclotella* sp. 2, *Nitzschia closterium*); and Chlorophyta (*Stichococcus* sp.) were most important numberically (Table III.D-6). The phytoplankton community is typified by a very low diversity with usually from 5 to 10 species being observed in the samples monthly. One or two of these consistently dominated all other forms by an order or two of magnitude.

ii. Zooplankton: The zooplankton is composed of a great array of micro-and macroscopic animals ranging in size from a fraction of a millimeter to 30 to 50 mm (1.2 to 2 inches). There are permanent plankton (holoplankton and temporary plankton (meroplankton). The former are those animals completely adapted to a pelagic mode of existence, like copepods, mysids, and chaetognaths, and the latter are the transitory floating states such as eggs, larvae, and juveniles of the benthos and nekton. The meroplankton are often seasonal in occurrence and abundance.

Table III.D-6

PHYTOPLANKTON OF GOLETA POINT MARSH[a]

SPECIES	Number of Cells
Stichococcus sp.	144,600
Gymnodinium sp.	61
Gymnodinium ovulum	13
Cyclotella sp. 1	133,152
Cyclotella sp. 2	126,217
Glenodinium lenticula	5,163
Glenodinium paululum	434
Peridinium obiculare	1,249
Gyrodinium aureum	126,130
Gyrodinium sp. 1	390
Gyrodinium sp. 2	104
Massartia sp.	4,694
Crucigenia sp.	294
Nitzschia closterium	47,507
Dunaliella salina	2,405
Platymonas subcorilformis	601
Gonium sociale	161

Source: Riznyk, 1977.

[a]Summary of phytoplankton species recorded as a number of cells x 10^3/liter from the lagoon on the University of California at Santa Barbara Campus (Goleta Point Marsh). Values represent the total yearly average from three stations.

Although zooplankton are often assumed to be the primary consumer in Pelagic food webs, serving to transfer energy from phytoplankton to secondary consumers, they are relatively inefficient in the food chains of the shallow estuaries and bays. They usually graze on only 2 to 9 percent of the available phytoplankton production (Williams, Burdoch and Thomas, 1968). A number of factors have been suggested to explain this situation (Riley, 1967): 1) inefficient feeder occurred as the dominant species of zooplankton, 2) unmatched seasonal cycles of phyto- and zooplankton, 3) benthos competing directly with zooplankton for food, and 4) predation by other animals on zooplankton.

Composition of Zooplankton. As in the case of phytoplankton, the zooplankton of Mission Bay were also divided into major and minor contributors to the total population. The major constituents of the zooplankton include: *Noctiluca* (holozoic dinoflagellates), *Heliocladus* (radiolarians), tintinnids (ciliates), mollusk larvae, polychaete larvae, barnacle larvae, cladocerans, and copepods (Fairbanks, 1969). Copepods are the major constituents of all the plankton at all depths throughout the year in Mission Bay.

Although *Noctiluca* is one of the major constituents of zooplankton in Mission Bay, it was not recorded at all by Lackey and Clendenning (1965) from San Diego Bay, where more than 100 species of dinoflagellates and more than 30 species of colorless zooflagellates are known to occur.

The copepod is also the major constituent of zooplankton in Anaheim Bay. It consists of 12 species, but only five of them are major contributors, i.e., *Arcatia tonsa, Paracalanus parvus, Labidocera trispinosa, Oncea minuta*, and *Corycaeus* sp. (Howey, 1971). Other frequently encountered holoplankton include cladocerans, ostracods, mysids, and pycnogonids. Some typical offshore holoplankton, such as hydromedusa, *Pleurobrachia* (ctenophore), *Tomopteris* (polychaete), *Sagitta* (chaetognath), *Oikopleura* (Order Larvacea), and thaliaceans occur in the bay only on a limited basis. Meroplankton of crustacean larvae, fish larvae, and eggs and larvae of unidentified vertebrates and invertebrates are quite common in the bay.

Of the 12 families of fish larvae recorded by Snyder (1965) from Mission Bay, five species of major contributors constitute 94.7 percent of the total fish larvae collected. They are (in order of decreasing abundance): *Clevelandia ios, Engraulis mordax, Atherinopsis californiensis*, sciaenids (possibly *Cynoscion* sp.), and *Hyposoblennius* sp. Slawson's (1972) study on the cladocerans of Anaheim Bay showed an occurrence of only five species, with two of them, *Podon polyphenoides* and *Evadne nordani*, accounting for 90 percent of the total cladoceran numbers. These are some examples of the characteristic feature of estuarine plankton with large volume dominated by small number of species.

Factors Controlling Zooplankton Population. Among the various environmental factors, temperature seems to be the most important in controlling the seasonal abundance of zooplankton in Anaheim Bay (Slawson, 1972; Sowby, 1973). Since the meroplankton derive mainly from the benthos, their presence will be controlled initially by the temperature requirements for adult spawning. Furthermore, the duration of the planktonic larval stage is also influenced by temperature. Generally within the favorable range, the lower the temperature, the slower is the larval growth which thus prolongs the planktonic stage. However, for a meroplankton contributor like the arrow goby (*Clevelandia ios*) in Mission Bay, which has a protracted spawning season, temperature does not seem to be a significant factor. The coefficient of correlation between temperature and number of larval goby computed by Snyder (1965) was only 0.11. On the other hand, like the greatest holoplankton contributor to the plankton community, *Acartia tonsa*, an eurythermal and euryhaline species, temperature is not a limiting factor of its presence and abundance in the bay.

Distribution of zooplankton in the bay seems to be controlled by the combination of tidal current and the degree of constriction of the bay opening. While the scarcity of offshore holoplankton in the bay was attributed to the constricture and limited circulation of water between the offshore area and the inner part of Anaheim Bay (Felts, 1973; Howey, 1971; Slawson, 1972), the tidal current alone accounted for the different patterns of meroplankton distribution in the same bay (Sowby, 1973). For instance, the larvae of pistol shrimp, *Crangon nigrimaculata*, are hatched offshore, but occur throughout Anaheim Bay, and the mudshrimp, *Callianassa* sp., an inhabitant of the bay, has its larval stages recorded offshore.

Although salinity is generally one of the major environmental factors in controlling the kinds, abundance, and distribution of zooplankton in the bays and estuaries, this is, however, not the case in Southern California, where low rainfall and less freshwater runoff minimize the fluctuation of salinity. Southern California coastal waters have an annual mean salinity of 34°/₀₀, but in the bays mean salinity is about 32.5°/₀₀. Therefore, practically all offshore forms can survive in the bays of Southern California.

Food availability does not appear to be a controlling factor of zooplankton population size and appearance. Most of the zooplankton are herbivores that feed on phytoplankton. It has been estimated that the estuarine zooplankton consume, at most, some 50-60 percent of the phytoplankton production; the remainder goes mainly to benthic fauna and flora. Fairbanks' (1969) study on the Mission Bay plankton showed that the increase in the standing crop of zooplankton did not always correlate with the decrease in that of the phytoplankton. Although decapod larvae are carnivorous meroplankton, their food items (copepods and cladocerans) occur and constitute throughout the year more than 50 percent of the total plankton volume in Anaheim Bay (Sowby, 1973). Therefore, even the carnivorous plankton are not controlled by food for their abundance and appearance in the bay.

Reaction to light with dirunal migration is prevalent in the offshore plankton. Although Snyder (1965) has collected in Mission Bay four times more fish larvae in the night sampling than in the day sampling, he did not attribute this result to the effect of light alone but to cumulative effects of light and tidal exchange.

Seasonal Fluctuation of Zooplankton Population. On the east coast of North America and the European coast, the most common and significant difference between estuarine and oceanic zooplankton is the relatively large summer population in the estuary. It is the result of a high level of primary production in the estuary and reflects the addition of numerous larvae of benthic invertebrates to the total plankton volume (Riley, 1967). In Anaheim Bay and Mission Bay, however, the peak of zooplankton population occurs mainly in the winter and spring months (Figure III.D-10). This seasonal difference in the peak plankton volume from the east coast is attributable to the early appearance of larvae of the benthic invertebrates along the California coast (Painter, 1966; Sowby, 1973). However, if the contribution of meroplankton to the total plankton community is considered according to their phylogenetic groups, a different picture emerges. The mollusk and barnacle larvae have peak appearances in the summer but the polychaete larvae were found as a major constituent only in November (Fairbanks, 1969).

c. Benthic Community: The benthic community includes all the organisms that live on or in the bottom of a given water body. The fouling organisms that commonly occur in the harbor and marina are also included in this community. Since the flora of this community have been treated (Section a.i), this section is devoted to the fauna.

Bacteria are both benthic and planktonic and have as much influence on the distribution of other plants and animals in the marsh and bay as have temperature, salinity, nutrient concentration, and other physical and chemical parameters (Hedgpeth, 1957). Bacteria are important, on the one hand, in decomposing dead organic matter which supplies necessities of plant growth, such as nitrates, phosphates, carbon dioxide, etc., and, on the other hand, in serving as food for the various bottom-dwelling animals. Zobell and Felthm (1942) have noted that bacteria are much richer in the water and mud of a bay than in the waters of the open sea. In Mission Bay, the aerobic bacteria are not only abundant at the surface, but also occur in greater numbers than anaerobic bacteria to a depth of about 60 cm (23.4 inches) well below the depth of free oxygen. Some infaunal ciliates (*Euplotes*) and nematodes living in anaerobic bottom sediments may feed on these associated bacteria.

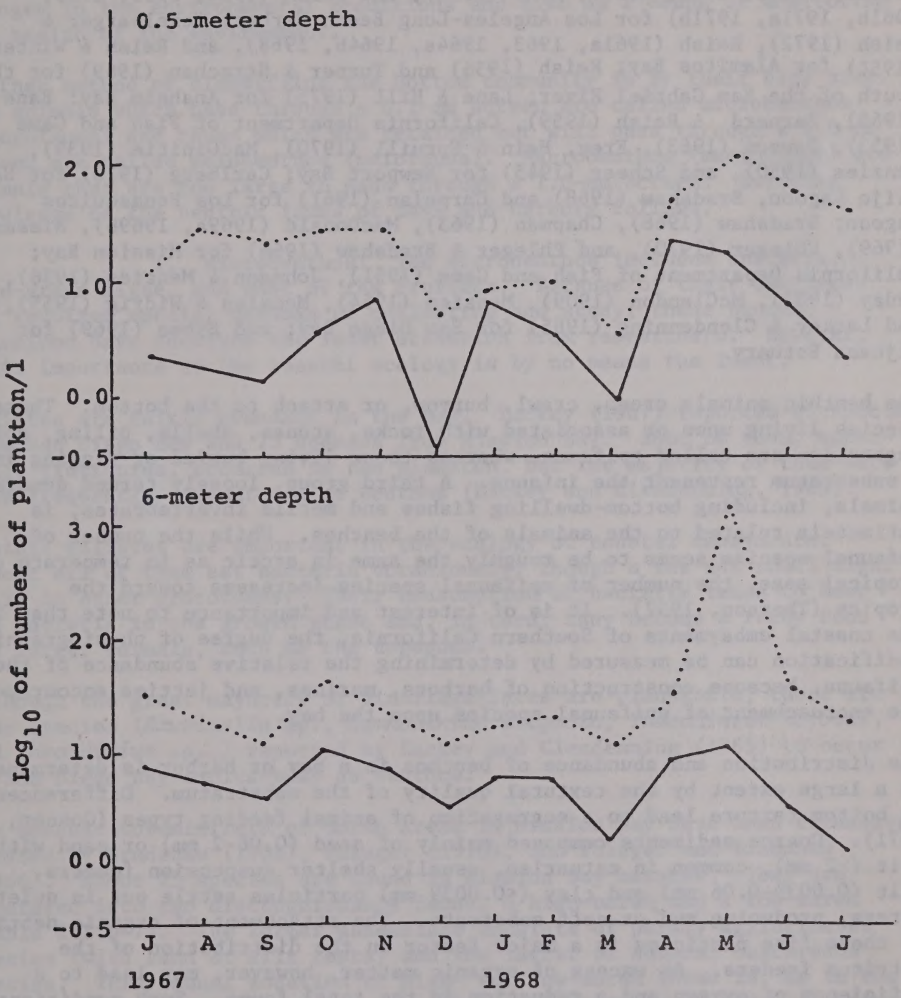


Figure III.D-10. Seasonal abundance of zooplankton and adult copepods in Quivira Basin, Mission Bay; . . . . . total plankton, _____ copepods (after Fairbanks, 1969).

Source: Ho (1974).

Information on the benthos of bays and harbors in Southern California are found in the works by Johnson (1971) and Reish (1965) for Marina del Rey; Anonymous (1952a), Barnard (1950, 1952, 1953, 1954, 1955, 1958), Barnard & Reish (1957, 1960), Hartman (1956), Horvath & Menzies (1951), Mensies (1951a, 1951b, 1952, 1957), Mohr (1953), and Reish (1954, 1955, 1959, 1961b, 1971a, 1971b) for Los Angeles-Long Beach Harbor; Eckelbarger & Reish (1972), Reish (1961a, 1963, 1964a, 1964b, 1968), and Reish & Winter (1954) for Alamitos Bay; Reish (1956) and Turner & Strachan (1969) for the mouth of the San Gabriel River; Lane & Hill (1975) for Anaheim Bay; Bane (1968), Barnard & Reish (1959), California Department of Fish and Game (1953), Dawson (1963), Frey, Hein & Spruill (1970), MacGinitie (1939), Menzies (1950), and Scheer (1945) for Newport Bay; Carlberg (1970) for San Elijo Lagoon, Bradshaw (1968) and Carpelan (1961) for Los Penasquitos Lagoon; Bradshaw (1968), Chapman (1963), MacDonald (1969a, 1969b), Niesen (1969), Phleger (1970), and Phleger & Bradshaw (1966) for Mission Bay; California Department of Fish and Game (1951), Johnson & Menzies (1956), Juday (1907), McClendon (1909), Menzies (1954), Menzies & Widrig (1955), and Lackey & Clendenning (1965) for San Diego Bay; and Bybee (1969) for Tijuana Estuary.

The benthic animals creep, crawl, burrow, or attach to the bottom. Those species living upon or associated with rocks, stones, shells, piling, and vegetation are called epifauna, whereas those living buried or digging in a substratum represent the infauna. A third group, loosely termed demersal animals, including bottom-dwelling fishes and motile invertebrates, is intimately related to the animals of the benthos. While the number of infaunal species seems to be roughly the same in arctic as in temperate or tropical seas, the number of epifaunal species increases toward the tropics (Thorson, 1957). It is of interest and importance to note that in the coastal embayments of Southern California, the degree of physiographic modification can be measured by determining the relative abundance of the epifauna, because construction of harbors, marinas, and jetties encourages the encroachment of epifaunal species upon the bay.

The distribution and abundance of benthos in a bay or harbor is determined to a large extent by the textural quality of the substratum. Differences in bottom texture lead to a segregation of animal feeding types (Gosner, 1971). Coarse sediments composed mainly of sand (0.06-2 mm) or sand with grit (>2 mm), common in estuaries, usually shelter suspension feeders. Silt (0.0039-0.06 mm) and clay (<0.0039 mm) particles settle out in quiet waters, producing mud or soft substrate. The attachment of organic debris to these fine particles is a major factor in the distribution of the detritus feeders. An excess of organic matter, however, may lead to a deficiency of oxygen and a reduction in the total fauna. Such conditions are often indicated by the blackening of subsurface layers, which is taken to indicate the presence of anaerobic bacteria.

The benthic community, particularly the infauna, generally reflects the condition of the environment not only at the time of sampling but also prior to sampling. Accordingly, Reish (1961b) proposed the importance of the knowledge of benthic animal composition in serving as an indicator of changes in the environmental conditions and also as a means of monitoring the health of the environment.

Another method of classifying the bottom community is by their body size. The animals which pass through a 0.1-mm screen are called microbenthos (microfauna) and those which are retained but will pass through a 1.0-mm screen are called meiobenthos (meiofauna). Macrobenthos (macrofauna) are animals that are too large to pass through a 1.0-mm screen. Existing knowledge of the benthic fauna of bays and harbors follows.

i. Microbenthos: The microbenthos includes bacteria, blue-green algae, and most of the Protozoa. Because of their smallness and required special methods of collecting and study, these benthic organisms have received the least attention from researchers. However, their importance to the coastal ecology is by no means the least.

Ciliates are fairly abundant in the bay. Lackey (1967) reported 41 species from San Diego Bay and 23 species from Mission Bay. Some of them, especially tintinnids, occurred in the plankton, but the majority of them were more frequently encountered as benthos (Lackey and Clendenning, 1965).

Benthic ciliates are important in the ecology of coastal embayments. Almost all of them eat bacteria voraciously, though a few eat small algal cells or other protozoans. Their consumption of bacteria tends to keep the bacteria in the growth phase and, in turn, they become a ready food for larger animals, such as the copepods.

Although the great majority of dinoflagellates are planktonic, there are four species (*Exuviaella* sp., *Gymnodinium stigmata*, *Thecadinium kofoidi*, and *Thecadinium* sp.,) reported by Lackey and Clendenning (1965) to occur in San Diego Bay exclusively as benthos.

The benthic foraminifera of marsh areas in Mission Bay have been extensively studied by Bradshaw (1968), Phleger (1970), and Phleger and Bradshaw (1966). About 25 species are found in Mission Bay marshes. They are separated into two distinguishable fauna, a high-marsh and a low-marsh (Table III.D-7). The former assemblage consists of purely agglutinated species (with sand or silt tests) and the latter of several calcareous species. This faunal zonation of high- and low-marsh forms is, as in the case of vegetal zonation, related to elevation, amounts of tidal flooding, and exposure (Phleger, 1970). The standing crops of these foraminifera vary greatly, but generally, the largest stocks are found in the high marsh and the smallest, on the tidal flats (see Figure III.D-8).

Table III.D-7

GENERALIZED DISTRIBUTION OF MARSH FORAMINIFERA
ON THE PACIFIC COAST OF NORTH AMERICA

SPECIES	Tidal Flat	Marsh Channel	Spartina Zone	Salicornia Zone
Ammonia beccarii	xxxxxx	xxxxxx		
Ammotium salsum	xxxxxxxxxxxxxxxxxx			
Arenoparella mexicana			xxxxxx	xxxxxx
Discorinopsis aguayoi		xxxxxx	xxxxxx	xxxxxx
Elphidium spp.	xxxxxx	xxxxxx		
Jadammina polystoma	xxxxxx	xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx		
Miliammina fusca	xxxxxx	xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx		
Textularia earlandi	xxxxxx			
Trochammina inflata		xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx		
T. macrescens			xxxxxxxxxxxxxxxxxxxx	

Source: Phleger & Bradshaw, 1966.

ii. Meiobenthos: As defined by Hulings and Gray (1971) and mentioned earlier, the term "meiofauna" generally is used to refer to animals that can pass a 1.0-mm screen. This is a relatively new definition as older literature considered the meiobenthos to be smaller. In his exhaustive treatment of estuarine benthos, Carriker (1967), reported meiobenthos to be those invertebrates which are retained by roughly a 0.1 to 0.5-mm opening mesh. This difference is important to remember because the groups of invertebrates reported to comprise the majority of the meiobenthos were of smaller size than those in newest definition. On the basis of the presence or absence of the resistance of the integument to mechanical damage, the meiofauna is further divided into "soft" and "hard" fauna. The former includes Ciliata, Cnidaria, Turbellaria, Gnathostomulida, Nemertina, Gastrotricha, Archiannelida, Polychaeta, Oligochaeta, Mollusca, and Echinodermata; and the latter, Foraminifera, Kinorhyncha, Priapulida, Nematoda, Bryozoa, Brachiopoda, Mystacocarida, Ostracoda, Copepoda, Palpigradida, Halacaridae, Tardigrada, and Tunicata. Some groups, like Cnidaria, Mollusca, Bryozoa, Brachiopoda, Echinodermata, and Tunicata are rather rare in the meiofauna. Nematoda and Copepoda are the most abundant and are frequently encountered meiobenthos; together they comprise 89 to 99 percent of the total meiofauna (Wieser, 1960).

Animals of the meiobenthos all tend to be in the size of 0.5 to 1.0 mm and are often very elongated, to enable them to fit in between sand and mud particles. Since they live largely between and on sediment particles, they are sometimes called "interstitial" fauna, especially those from sandy environments.

Carriker (1967) pointed out that the meiobenthos could be separated into three ecological groups according to their various degrees of affinity with the sediment particle size, i.e., sand-dwelling species, fine deposit-dwelling species, and eurytopic species. Thus, the meiobenthos at any point in the bay is determined by the degree of mixing of sediment types, to which it is quite sensitive, and consists of a subtle graded series of faunal assemblages. Most meiobenthic organisms feed on the epigrowth of sand grains or on the fine deposits, which further affects their distribution.

The nematodes generally occur in greatest number in the top 5 cm (2 inches) of sediment. Large populations of nematodes have been found living in the interstitial water within mud and sand in the bays of Southern California (Frey, Hein and Spruill, 1970; Reish, 1968, 1972), but species identifications were not given in the studies. Although this is perhaps the most abundant group of animals of all benthos, it is also the least studied. The reasons for this disparity are manifold and complex, but the most important single reason is probably the difficult nature of marine nematode systematics (Hope, 1971).

Although some pelagic species of ostracods were recorded in plankton samples in San Diego Bay (Juday, 1907), the great majority of them live on or near the bottom, or in some cases in the upper few millimeters of the bottom sediments, through which they root and burrow after food. The nature of the bottom sediments is, therefore, of extreme importance in determining the species of ostracod. As in the case of the nematodes, this is another little known group of meiobenthos in the Southern California bays, yet their abundance in the bay is not negligible. Klingbeil (1972) has reported that the topsmelt, *Atherinops affinis*, was the most frequently captured fish in Anaheim Bay, and in the larger specimens, ostracods were the most frequent organism seen in the gut contents, occurring in more than 80 percent of the catch.

According to Warme (1971), *Xestoleberis aurantia* is the only ostracod abundant on the marsh and present in all environments below the marsh except the large sandy channels. It is the most common ostracod that occurred in the samples from Upper Newport Bay and Mugu Lagoon. Warme also reported that several species of *Cyprideis*, *Loxocomcha*, *Bradleya*, and *Cythereis* known from Todos Sanos Bay, Baja California, were found or were likely to be found in Mugu Lagoon. If this is the case, the same species may be found in the bays and lagoons of the other areas of Southern Californi as well.

It is important to mention that an as yet undescribed cephalocarid crustacean has been found in Anaheim Bay. So far, only one intact specimen has been collected from the intertidal mud flats near Hog Island in the bay

(Lane, 1975). Since several subsequent attempts to find this crustacean from the bay have been unsuccessful and only a few specimens ever have been found in the stomach contents of arrow gobies in the bay, this cephalocaridean could be one of the rarest meiobenthos living in Anaheim Bay. The cephalocarids are the most primitive living crustacean and to date only three genera and eight species are known to exist. A systematic study of this new Cephalocarida is underway.

iii. Macrobenthos: Animals considered as macrobenthos include both invertebrates and vertebrates. Generally, because of their conspicuousness, this group is better known than the micro- or meiobenthos. In most works on the faunal surveys of bays and harbors, the species recorded and identified are mainly of this group. However, small macrobenthos, such as turbellarians, nemerteans, and certain crustaceans, are still not very well known.

The invertebrate macrobenthos in the bay can be suspension feeders, detritus feeders, or predators, but the vertebrates, mainly benthic fishes, are largely carnivores. The feeding habits of macrobenthos are known to be closely related to the sediment types (Carriker, 1967). The detritus feeders predominate in areas of slow currents in the bay that have silt deposition; the suspension (filter) feeders exceeded detritus feeders in all areas of the bay where the grain size is of fine sand (0.1-0.25 mm); and the largest standing stock of predators occur in high energy environments where the sediment size surpassed fine sand and the contents of clay and organic matter are generally low.

Invertebrates. Because of their importance as indicators of bottom conditions (Reish, 1964a), polychaetous annelids are the most studied animals of all the macrobenthos in some Southern California bays and harbors. Amphipods and mollusks are perhaps the only other groups that have received much attention in the past. However, almost all of the previous surveys and studies were conducted on the macrobenthos of bays and harbors in Los Angeles and Orange Counties and very little was done on those in the embayments of San Diego County (see Table III.D-8).

According to Kauwling and Reish (1975), the polychaete diversity is about equal in the four studied embayments of Southern California, i.e., Los Angeles-Long Beach Harbors, Alamitos Bay, Anaheim Bay-Huntington Harbor, and Newport Bay. Since the number of species found in a study area depends to a large extent on the number of stations and the number of visits to each station, the figure given in Table III.D-8 for San Diego Bay cannot be used for this comparison of species diversity except in a most general way.

Table III.D-8

NUMBER OF SPECIES OF THREE MOST-STUDIED GROUPS
OF INVERTEBRATE MACROBENTHOS KNOWN
FROM SOUTHERN CALIFORNIA EMBAYMENTS

LOCALITY	Polychaeta	Amphipoda	Mollusca
Los Angeles-Long Beach Harbor	69	11	54
Alamitos Bay	77	13	49
Anaheim Bay	76	7	54
Newport Bay	61	34	74
Mission Bay	?	?	19
San Diego Bay	17	?	25
Tijuana Estuary	?	?	10

Source: Compiled from various sources.

Thirteen species and two genera of polychaetes are commonly encountered in the bays (Table III.D-9). These taxa were so prevalent that one could probably describe the benthos of any Southern California embayment as being characterized by several or all of them. However, many less frequently occurring species were collected from only one area, especially from the upper reaches of each embayment (Reish in Barnard and Reish, 1959). Kauwling and Reish have concluded further that all the prevalent species of polychaetes were distinctly more abundant in one area or the other. The single most common polychaete species in Southern California's bays and harbors is probably *Capitita ambisita*, which was found in all studies and usually in substantial numbers. Although an extensive survey on the polychaete fauna of San Diego Bay is yet to be made, the existing record (California Department of Fish and Game, 1951) shows that there is no occurrence of *Capitata ambisita*, and *Lumbrineris erecta* replaces the status of *Lumbrineris minima*.

A cosmopolitan species of polychaete, *Capitella capitata*, was discovered by Reish (1955) to be an indicator of pollution in the Los Angeles-Long Beach harbors (Table III.D-10). Barnard (1958) also pointed out that three species of cosmopolitan amphipods, *Corophium acherusicum, C. insideiosum*, and *Podocerus brasiliensis*, were also indicators of pollution in the same harbor. These species can thrive in many parts of the harbor where other species of polychaetes and amphipods do not live.

Table III.D-9

RELATIVE ABUNDANCES OF COMMON POLYCHAETES
OF SOUTHERN CALIFORNIA EMBAYMENTS

GENUS-SPECIES[a]	L.A.-L.B.[b] Harbor	Alamitos Bay	Anaheim Bay	Newport Bay
Capitata ambiseta	+	**	**	**
Lumbrineris minima	+	*	+	*
Haploscoloplos elongatus	+	*	+	*
Capitella capitata	**	**	+	**
Cossura candida	**	*	**	**
Stauronereis rudolphi	*	**	+	**
Tharyx sp.	**	**	+	*
Prionospio cirrifera	+	+	**	*
P. b. newportensis	+	*	+	*
Armandia bioculata	+	+	*	*
Streblospio benedicti		**	**	+
Polydora spp.	+	*		+
Cirriformia luxuriosa	*	+	*	
Euchone limnicola		**	+	
Nerinides acuta		+	+	+
Neathes succinea		*	+	

Source: Modified from Kauwling and Reish, 1974).

[a]Arranged in approximate order of decreasing importance.

[b]** = major, * = important, + = present.

Table III.D-10

CONDITIONS OF FIVE ECOLOGICAL AREAS OF LOS ANGELES-LONG BEACH HARBORS

ECOLOGICAL AREAS	Domonant sp. of Polychaete	Dissolved Oxygen (ppm) (mean)	Organic Carbon (%) (mean)
Healthy bottom	*Tharyx parvus* *Cossura candida* *Nereis procera* *Polydora paucibranchiata*	6.0 3.2	2.5 2.0
Semihealthy bottom I	*Dorvillea articulata*		
Semihealthy bottom II	*Cirriformia luxuriosa*	3.2	2.7
Polluted bottom	*Capitella capitata*	3.5	2.7
Very polluted bottom	No species	2.2	3.4

Source: Modified from Reish (1959).

The most common amphipods occurring in Newport Bay are (Barnard and Reish, 1957): *Amphideutopus oculatus, Acuminodeutopus heterurupus, Rudilemboides stenopropodus*, and *Paraphoxus* sp. Although none of them is endemic to Newport Bay, a certain degree of "nativeness" is observed. They are not found in any abundance on the coastal shelves bordering the bay, and the several common species of *Ampelisca, Paraphoxus*, and *Photis* and other open-shelf amphipods are either missing or occur only as strays in Newport Bay. The dominant Newport Bay mud-bottom species are thought to be derived from open-sea depths below 10 mm (0.4 inches) and not from the intertidal region or soft bottoms shallower than 10 mm (0.4 inches). The introduction of these calm-water elements into the bay is correlated with the introduction of pilings on which they live (Barnard, 1961).

MacDonald (1969a, b) made a quantitative study of mollusks occurring in the marsh area of Mission Bay. He found that the creek fauna contained more variable species-composition than the marsh (Table III.D-11). A comparison with other marsh mollusk faunas of the Pacific Coast shows that the most abundant species, *Assiminea translucens*, in the Mission Bay marsh is the major gastropod of the Pacific Coast. The next abundant species, *Cerithidea californica*, which does not occur to the north of Point Conception, is close to its northern edge of distribution (see Figure III.D-11). The California horn snail, *C. californica*, is also abundant in Anaheim and Newport bays; the snail was reported to harbor 18 species of parasitic trematode larvae (Martin, 1972).

The standing crop of the marsh mollusk fauna in Mission Bay, indicated by biomass (dry weight in gram/m^2), remained almost constant but that of the creek fauna showed a marked seasonal variation, being highest in the summer. This variation results from changes in the abundance of *C. californica* and may reflect a seasonal migration of this species to lower elevations for breeding purposes.

The cosmopolitan species of mussel, *Mytilus edulis*, is very abundant in quiet-water of bays where there is hard substrate. It is one of the major fouling organisms occurring in the harbor. The community of *Mytilus edulis* is rich in epifauna. In Alamitos Bay, Reish (1964b) identified five species of algae, 22 species of ectoprocts, and six species of tunicates associated with this bay mussel. A direct relationship between the number of associated species and water temperature was observed; the warmer the water, the greater was the diversity of species composition. Some species occurred in the mussel community throughout the year without seasonal fluctuation; others occurred with definite spring or summer peak; and still others occurred only seasonally, either in spring or summer.

The populations of sand dollar, *Dendraster excentricus*, occurring in the sand flat areas of Mission Bay Channel and Tijuana Estuary were studied by Niesen (1969). A comparison with the offshore population (of La Jolla Shores) indicated that there were differences in population size and size structure; the bay population was larger (about 25 individuals per 0.1 m^2), remained stable with little fluctuation in size structure, and consisted of relatively larger robust individuals (65.7 $\pm$ 0.85 mm). These differences between the bay population and the outer coastal subtidal populations were attributed by Niesen to the variance in the water movement, amount of food, and feeding behavior.

As part of the BLM baseline studies, Straughn (1976) sampled three intertidal marsh areas, Salt Creek, Santa Margarita Bay, and Mugu Lagoon. Twin Harbors at the Isthmus of Santa Catalina Island also was sampled, but was somewhat unusual, probably because its open communication with the sea allowed the occurrence of species typical of both the open ocean sandy beaches, and semienclosed bays.

Table III.D-11

SPECIES COMPOSITION AND RELATIVE ABUNDANCE (%)
OF MOLLUSKS IN MISSION BAY

GENUS-SPECIES	Tidal Marsh Fauna	Tidal Creek Fauna
Gastropoda		
Acteocina culcitella	2.0	68.7
Assiminea translucens	68.6	+
Bulla gouldiana		+
Cerithidea californica	28.2	28.2
Littorina planaxis	+[a]	
L. scutulata	+	
Melampus olivaceus	0.9	
Nassarius tegula		1.4
Siphonaria brannani		+
Pelecypoda		
Chione fluctifraga	+	0.6
C. undatella		*
Cryptomya californica		*
Macoma nasuta		*
Modiolus senhousei		0.6
Mytilus edulis	*[b]	*
Lyonsia gouldii		+
Ostrea lurida	*	
Protothaca staminea		0.2
Tagelus californianus		0.3
Total individuals	2,153	5,462
Number of samples	100	78
Marsh area (km^2)	0.139	0.003

Source: Modified from MacDonald, 1969).

[a] + = present but less than 0.1% individuals per site.

[b] * = present at site but did not occur in samples.

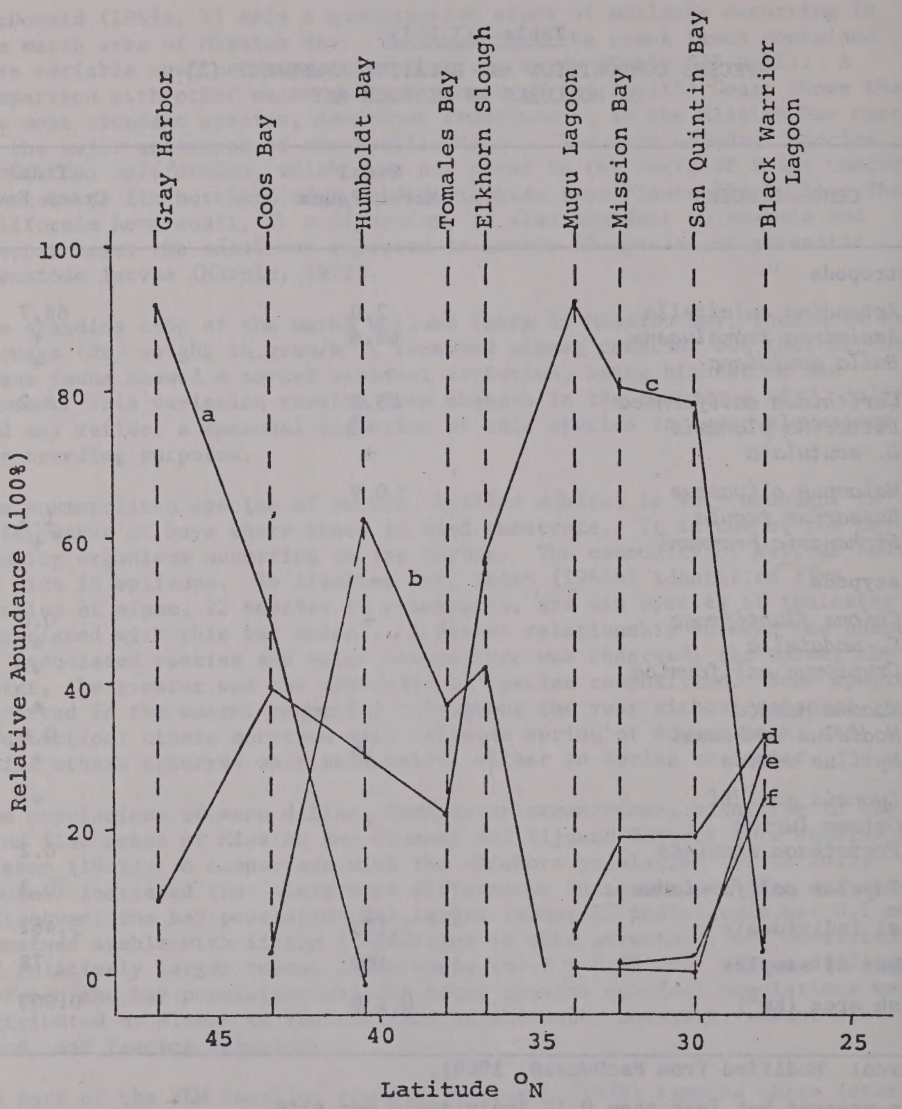


Figure III.D-11. Latitudinal changes of relative abundance of six species of salt marsh mollusks on Pacific Coast of North America (after MacDonald, 1969). a = *Littorina newcombiana*, b = *Phytia myosotis*, c = *Assiminea translucens*, d = *Cerithidea californica*, e = *Melampus olivacens*, f = *Acteocina culcitella*.

Source: Ho (1974).

The marsh or slough sites appeared to be governed by different factors, perhaps including greater dependence on biotic interactions. Each of the three sloughs appeared to have a characteristic species complement (Figure III.D-12) overlapping range of salinities. The observed range of salinities reflects changing exposure to seawater intrusion of freshwater inflow from water courses and runoff. Mugu Lagoon which is open to the ocean all year averages 35°/$_{oo}$, while Santa Margarita, which is a river estuary open only seasonally to the ocean, ranged from 20 to 32°/$_{oo}$. Salt Creek is also closed most of the year but does not have much freshwater inflow and therefore exhibits elevated salinities (averages ranging from 35 to 40°$_{oo}$) as a result of evaporation. It is obvious that although marsh sediments must undergo shifting from time to time as rivers or the ocean cut an opening at the mouth, radical instability resulting from wave impact did not appear to be a prominent feature of the estuarine environment.

Vertebrates. Anaheim and Newport Bays are the only two embayments in Southern California where a systematic survey on the fish has ever been attempted. A total of 68 species was recorded from Anaheim Bay by Klingbeil, Sandell and Wells, (1975), and Dixon and Eckmayer (1975), and 61 species from Newport Bay by Bane (1968) and Frey, Hein and Spruill (1970). As expected, the fish fauna of these two bays are comparable, with more abundant species generally being common to both bays and very few species that are common in one bay but relatively rare in the other. All fishes recorded from the bays are not, in the strict sense, benthic forms. Some fishes, like flatflash and goby, are true macrobenthos; other, like killifish, topsmelt, and surfperch, although not strictly benthic in occurrence, are closely associated with substrate in that they all feed on benthic invertebrates.

The arrow goby, *Clevelandia ios*, is a very common fish in the bays of Southern California. It is the most abundant species of the gobiids occurring in Anaheim Bay, living either free on the bottom or commensally in the burrows of the echiuroid worm, *Urechis caupo*; ghost shrimp, *Callianassa* sp.; or blue mudshrimp, *Upogebia pugettensis*. The pelagic larvae of this goby feed exclusively on the calanoid copepod, *Acartia tonsa*, whereas the adults, greater than 14 millimeters, are primarily benthic carnivores that feed on harpacticoids, cyclopoids, ostracods, nematodes, oligochaetes, and amphipods. They are in turn preyed upon by other larger carnivorous fishes (MacDonald 1975).

Anaheim Bay has high populations of two species of flatfish, the California halibut, *Paralichthys californicus*, and the diamond turbot, *Hypsopsetta guttulata*. It appears that the former feeds either on or above the substrate, whereas the latter feeds either on or in the substrate. Thus the two species

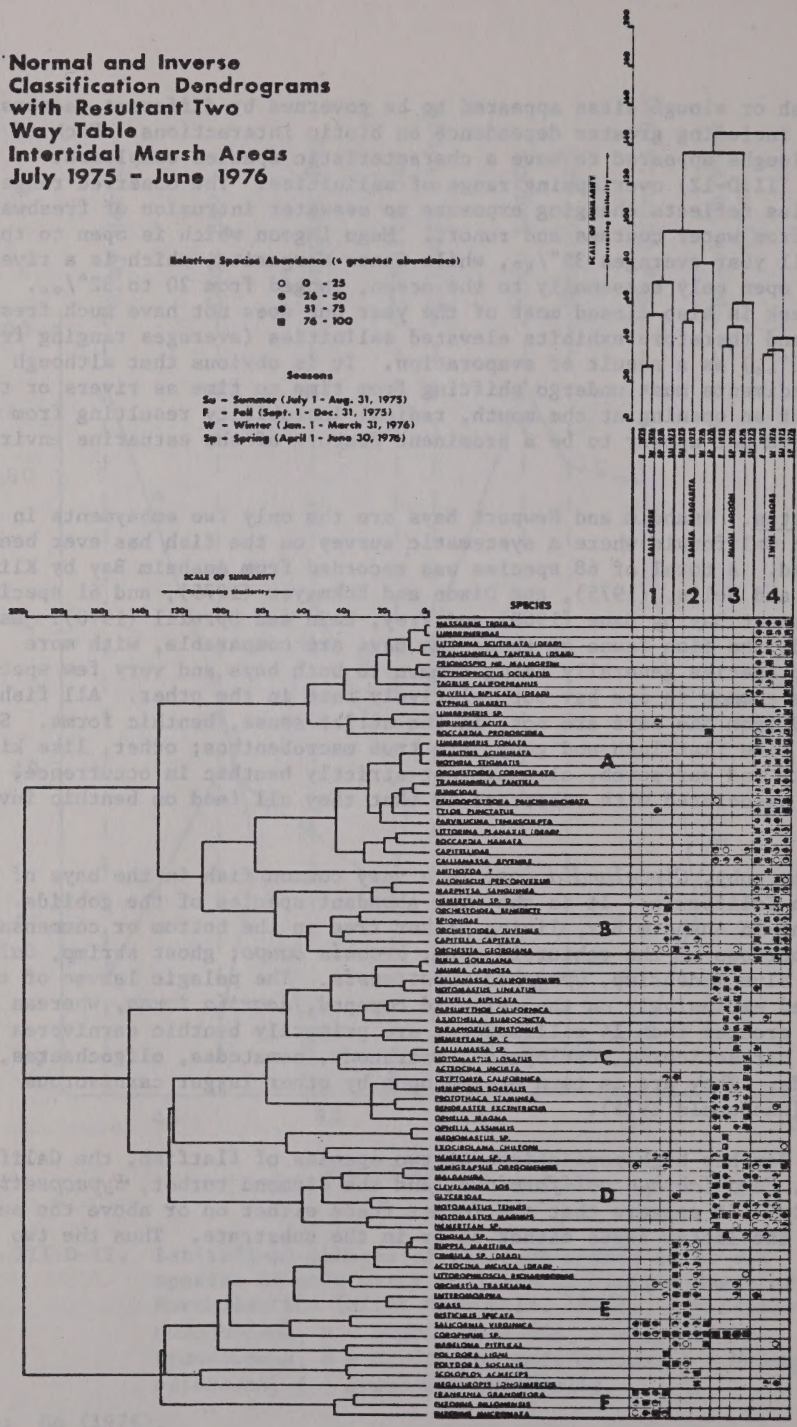


Figure III.D-12. Classification Dendrograms and Resultant Two-Way Table for Marsh Areas.

Source: Straughan (1977).

are ecologically separated insofar as competition for food is concerned. Studies on their stomach contents showed that the halibut fed mainly on fishes and crustaceans (Haaker, 1975) and the turbot mainly on mollusks, polychaetes, and crustaceans (Lane, 1975).

Carpelan (1961) made an observation on the fish in Los Penasquitos Lagoon with regard to their salinity tolerance. The lagoon is a variable type that was open to the ocean during the first six-month period (July-December, 1957) of observation and closed off during the following eight months. While pH and dissolved oxygen changed only slightly before and after the closure, salinity and temperature showed remarkable difference. The temperature difference was between 4 and 5°/$_{oo}$ to over 60°/$_{oo}$. *Hypsopsetta guttulata* withstood change a little longer until 60°/$_{oo}$ was reached. *Fundulus parvipinnis, Girella nigricans*, and *Atherinops affinis* were still thriving at 63°/$_{oo}$ when the observation was terminated.

d. Permanent Dwellers and Seasonal Visitors: According to the amount of their lifetime being spent in the bay, animals occurring in the embayment can be separated into permanent dwellers and seasonal visitors. Most of the animals living in the bays and lagoons are recruited originally from the sea. They enter the bay either as adults to spawn, mate, or feed or as larvae to settle down. This recruitment of bay community may be year-round, as in those species that only breed at certain times of the year.

Nektonic species (mostly fish) can move in and out of the embayment independently of the tidal current, but meroplankton rely entirely on the tidal current for their immigration and emigration. In Southern California bays and lagoons, salinity characteristically does not constitute an important factor in controlling the recruitment of neritic members; other parameters, such as temperature, dissolved oxygen, food, and sediment condition, control the composition of the community and abundance of each member in the community. The constricture of the bay mouth is particularly important in limiting the immigration and emigration of meroplankton.

The permanent dwellers are the major members of the bay community, which consists of all of the sessile invertebrates, the infauna, the tubicolous animals, and some fishes typically found in the bay.

i. Invertebrates: The bay mussel, *Mytilus edulis*, is perhaps the most conspicuous permanent dweller of the harbors and marinas where hard surface is readily available. Upon establishment, the mussel provides a community to the bay with an assemblage of more than 60 species of various permanently dwelling macroinvertebrates (Reish, 1964b). On the soft bottom of Anaheim and Newport Bays, however, the ghost shrimp, *Callianassa* sp.; the striped shore crab, *Pachygrapsus crassipes*; and the California horn snail, *Cerithidea californica*, are the most conspicuous permanent invertebrate dwellers.

Although the epifauna typically associated with the eelgrass, *Zostera marina*, in Anaheim and Newport Bays are yet to be studied, works from other areas indicate that the eelgrass community in an embayment maintains a rich population of many permanent dwellers. Marsh (1973) recorded more than 100 species of organisms associated with the eelgrass in an estuary in Virginia; this complex epibenthic community was quantitatively and qualitatively distinct from others in the area.

The isopod gribble, *Limnoria tripunctata*, is a serious woodboring pest in the harbors where the waters have become polluted and where salinities are not markedly reduced by influx of freshwater. Isopods are generally considered an inhabitant of shallow water, but once established in a harbor, they quickly become a permanent dweller. Although they do not migrate out of the harbor, an extensive migration within the harbor has been observed. Johnson and Menzies (1956) found that *L. tripunctata* underwent a definite seasonal migration in San Diego Harbor. The migratory period reaches its height approximately during the season of highest water temperature (June and July) and the sexually mature adults make up about 97 percent of total migrant population. Most migrant females appear to have produced a brood prior to migration, and at the time of migration they are not gravid. The factors influencing migration are probably a combination of approach to a reproductive phase and population pressure from overcrowding in an old established population.

Insects are quite different from other animals of coastal embayments in that they are all originated from freshwater. Their abundance in salt marshes is very remarkable. Davis and Gray (1966) found some 250 species of insects on North Carolina salt marshes and concluded that they were abundant in both variety and quantity. Studies on the insects of salt marshes in Southern California are particularly scanty. Cox's (1969) study on the euryhaline water boatman, *Trichocorixa reticulata*, found in San Diego Bay, Mission Bay, Del Mar Lagoon, and San Elijo Lagoon is perhaps the only existing work on this subject. The water boatman is a permanent dweller of these bays and lagoons. It is generally a bottom dwelling insect, living in shallow, stagnant waters and coming to the surface only to replenish the gas film which envelops most of the body. It is primarily a detritus feeder but can filter feed on small plankton. Cox found that the nymphs were almost always present throughout the year in the bays and lagoons surveyed.

The sand dollar, *Dendraster excentricus*, is a permanent dweller of the bays. Several populations were observed by Niesen (1969) for a year in San Diego regions. It was noted that at almost all times, the sand dollars in Mission Bay remained in the upright position with their bodies oriented perpendicularly to the flow of the tidal current that came into the bay. This upright positioning of sand dollars forms a bed that provides an ideal shelter for many invertebrates. The species composition of these

beds seems to reflect the locality of the population, e.g., the anthozoan coelenterates and asteroids are associated only with the open shore beds but not with the estuarine beds (Table III.D-12). This list should be compared with that of shallow water soft bottoms in Section II.E.a.i.

ii. Vertebrates: Four of the seven most common teleosts recorded from Anaheim Bay are permanent dwellers in that bay. They are the topsmelt, *Atherinops affinis*; the California killifish, *Fundulus parvipinnis*; the arrow goby, *Clevelandia ios*; and the diamond turbot, *Hypsopsetta guttulata*. Studies on the life history of these fishes by Klingbeil (1972), Fritz (1975), Macdonald (1975), and Lane (1975) have shown that they complete their life cycle in the bay.

According to Haaker (1975), Anaheim Bay is used by California halibut, *Paralichthys californicus*, for a nursery ground. The young fish, about 12 to 40 mm (1.6 inches) long, come into the bay during April and May. They stay in the bay until they grow to about 200 mm (7.8 inches) long. Their emigration from the bay is assumed to be a maturation-oriented movement. Another species of very common teleost, the Pacific staghorn sculpin, *Leptocottus armatus*, also uses the bay as a nursery area. Tasto (1975) found that the bay population of the staghorn sculpin consisted almost entirely of juvenile fish less than a year old.

The shiner perch, *Cymatogaster aggregata*, is also a very common fish of Anaheim Bay. Although it is a permanent dweller of the bay, shiner perch exhibit a definite seasonal movement within the bay. They stay in the inner bay for most of the year but move out in the summer to shallow beach within the outer harbor (Dixon and Eckmayer, 1975). The shiner perch is a viviparous fish that is ready to bear its young in May (Odenweller, 1975). Therefore, this movement in the bay during summer is a breeding migration.

The deepbody anchovy, *Anchoa compressa*, is a typical seasonal visitor to Anaheim Bay. The adults come into the bay for spawning during the summer months. Since none of them was collected from November to March (Klingbeil, 1972), it is assumed that the spent adults either move out of the bay or die soon after spawning.

The gray smooth hound, *Mustelus californicus*, is abundant in shallow water off Southern California and is the most common elasmobranch (fish of the class that includes sharks and rays) found in Anaheim Bay. Although there is no apparent diel pattern of abundance in the bay, a seasonal trend has been observed with two distinct peaks, a greater one in the spring and a lesser one in the summer (Sandell, 1973). It seems that the shark uses the bay as a mating and breeding ground and moves in and out of the bay readily when there is a drastic change in the environmental condition. The lack of capture of this shark in the bay in August, 1971, was attributed by Sandell to the outbreak of a red tide. The shark may have moved out of the bay through direct response to low dissolved oxygen or as an indirect

Table III.D-12

INVERTEBRATES ASSOCIATED WITH SAND DOLLAR
Dendraster excentricus, BEDS IN SAN DIEGO REGION

ASSOCIATED SPECIES	La Jolla Shores	Mission Bay	San Diego R. Flood Channel	Tijuana Estuary
Anthozoa				
Harenactis attenuata	x			
Renilla kollikeri	x			
Stylatula elongata	x	x		
Zoalotus actius	x			
Gastropoda				
Astraea undosa		x		
Balcis sp.	x			
Bulla gouldiana			x	x
Conus californicus			x	
Kelletia kelletia		x		
Nassarius fossatus	x	x	x	x
Navanax inermis			x	x
Olivella biplicata	x	x	x	x
Polinices recluzianus	x	x	x	x
Pelecypoda				
Protothaca staminea			x	x
Siliqua patula				x
Tagelus californianus			x	x
Decapoda				
Callianassa californiensis			x	
Cancer spp.				x
Hemigrapsus oregonensis				x
Heterocrypto occidentalis				
Loxorhynchus cripsatus		x		
Portunus xantusii	x	x	x	x
Pachygrapsus crassipes		x		x
Asteroidea				
Astropecten armatus	x	x		
Patiria miniata		x		
Pisaster giganteus	x	x		
P. ochraceus		x		

Source: Compiled from Niesen, 1969.

result of lack of food. This shark was also observed to move out of the bay in the winter when the water temperature dropped below 11°C.

The marshlands and mud flats of bays and lagoons attract many species of birds. These areas are an excellent habitat for residential birds and an ideal resting and feeding area for migratory shorebirds and water birds. More than 150 species of birds have been seen in Anaheim Bay, 158 species in Upper Newport Bay, about 200 species in Buena Vista Lagoon, and 128 species in San Elijo Lagoon (Carlberg, 1940; Speth, 1969). Based upon the 1967-68 census conducted by the California Department of Fish and Game, a conservative estimate of close to 4 million bird-days-use was calculated for Upper Newport Bay. The shorebirds accounted for 74 percent of this use and the ducks for the other 26 percent. The greatest use was found to occur from mid-September to April; e.g., on February 14, 1968, an estimated 56,250 birds were tallied, but by June 14, 1968, the count was only 550 birds (Frey, Hein and Spruill, 1970).

e. Ecological Succession: Generally, much less is known about the succession of communities in marine environments than in the terrestrial or freshwater regions. Of a few studies made in regard to marine ecological succession, almost all were made either on the salt marsh flora or on the epifauna, particularly the fouling organisms of hard surface in the littoral zone. As to the succession of level-bottom community, infaunal community, and plankton community, practically nothing is known. This paucity could be because many marine ecologists have not kept in mind the concepts of the ecological succession and the climax community, or simply doubt its occurrence in marine communities (Hedgpeth, 1957).

i. Foral Succession in Marshland: According to his study on the salt marsh plants of San Diego County, Purer (1942) gave the following sequence for the succession of marsh flora. *Spartina*, the marsh plant that is most tolerant to water, is the pioneer. It grows on muddy surface, traps silt, accumulates dead parts of the grass, consolidates the mud, and eventually raises the surface to form a stable level habitat. Then, the *Salicornia* gains a foothold in this Spartinetum. As the area has less and less water standing on it continually, pickleweed is found in pure stands. The pickleweed does not survive where it is totally submerged; it needs some aeration in the soil. The next stage is that in the upper edge of Salicornietum, where *Batis, Monanthochloe, Distichlis*, and *Suaeda* appear. These plants are usually partly submerged daily. *Limonium* is associated with all of the above except *Batis*, which maintains itself on slightly lower flats. On higher ground there are various species of *Artriplex*, associated with *Frankenia* and above, out of the reach of the storm waves.

ii. Faunal Succession in Harbors: Basing his observations on the benthic fauna in a freshly excavated boat harbor in Alamitos Bay, Reish (1961a) reported that there was no indication of succession. The principal benthic species included 11 species of polychaetes, unidentified nemerteans, and one species of pelecypod; they were all dominant during the entire three-year period of study. However, Carriker (1967) has expressed doubt that an ecological succession had not been found in the benthic communities of the harbor.

Scheer (1945) found an occurrence of true succession in the fouling organisms of Newport Harbor. He argued that the basic problem in the development of a sequence of marine animal communities in a limited environment was that of distinguishing between seasonal progression and true succession. In the occurrence of a true succession, the early forms must drop out and be replaced by later forms; also, some of the earlier forms must be essential for the establishment of the later forms. If these conditions are not present then the development is a seasonal succession. Scheer's view on the sequence of community development in Newport Harbor is summarized in Figure III.D-13. According to him, a newly exposed surface is first colonized by bacteria, algae, and in some cases, hydroids. The development of these forms provides a favorable surface for establishment of bryozoan colonies and serpulids. The vigorous growth of the later forms eventually displaces the algae and hydroids. The resulting bryozoan community in turn provides a favorable basis for the attachment of *Mytilus* larvae. The growth of the mussels effectively covers the whole surface and eventually displaces the bryozoan community. Seasonal settlement of ascidian or barnacle larvae in tremendous numbers may introduce variations into this sequence. *Ciona* may sometimes colonize a clean surface, or one covered with algae, to such an extent that the bryozoans are unable to maintain their foothold. *Styela* apparently settles only on bryozoan substrate, but may become established before *Mytilus*. Sponges are frequently associated with *Styela*. The ascidian communities are eventually displaced by *Mytilus*.

The *Mytilus edulis* community in Alamitos Bay Marina and *Mytilus californianus* in Marina del Rey were, however, reported by Reish (1964a, 1965) to exhibit seasonal progression rather than true succession. When the float in Alamitos Bay was scraped free of all macroscopic life in late winter, *M. edulis* appeared in about a month, but when it was scraped in summer or early fall, the bay mussel did not appear until six to seven months later.

f. Productivity and Coastal Ecology: The inshore areas such as shallow seas, bays, lagoons, and estuaries are generally very productive. In favorable circumstances, net primary productivity may be comparable to a tropical rain forest (Mann, 1973). The bottom frequently supports a rich fauna, with benthic invertebrates alone often amounting to a standing crop biomass in excess of 100 grams of protoplasm (mainly

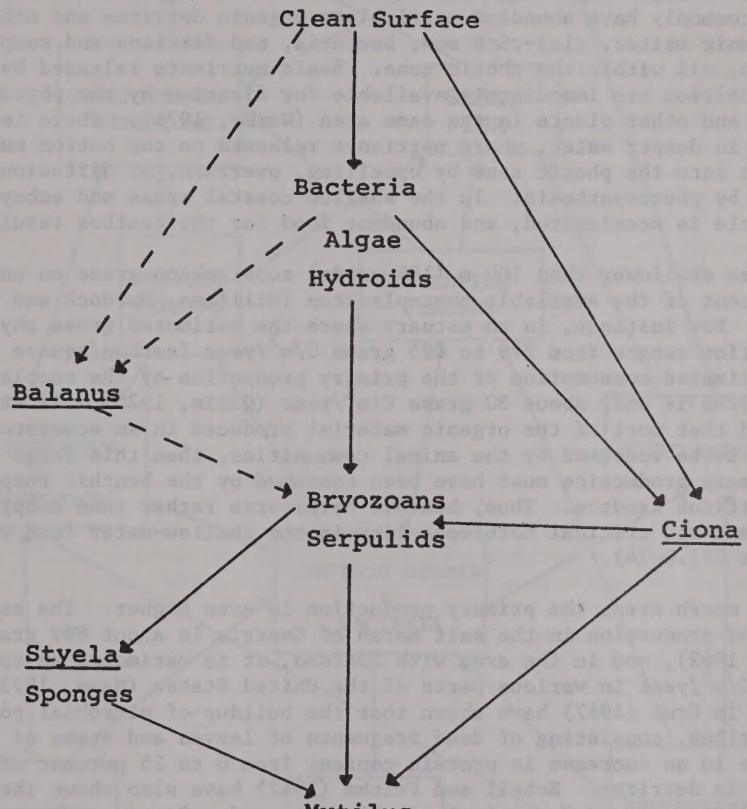


Figure III.D-13. Sequence of dominant organisms as appeared on hard surfaces exposed in Newport Harbor (from Scheer, 1945).

Source: Ho (1974).

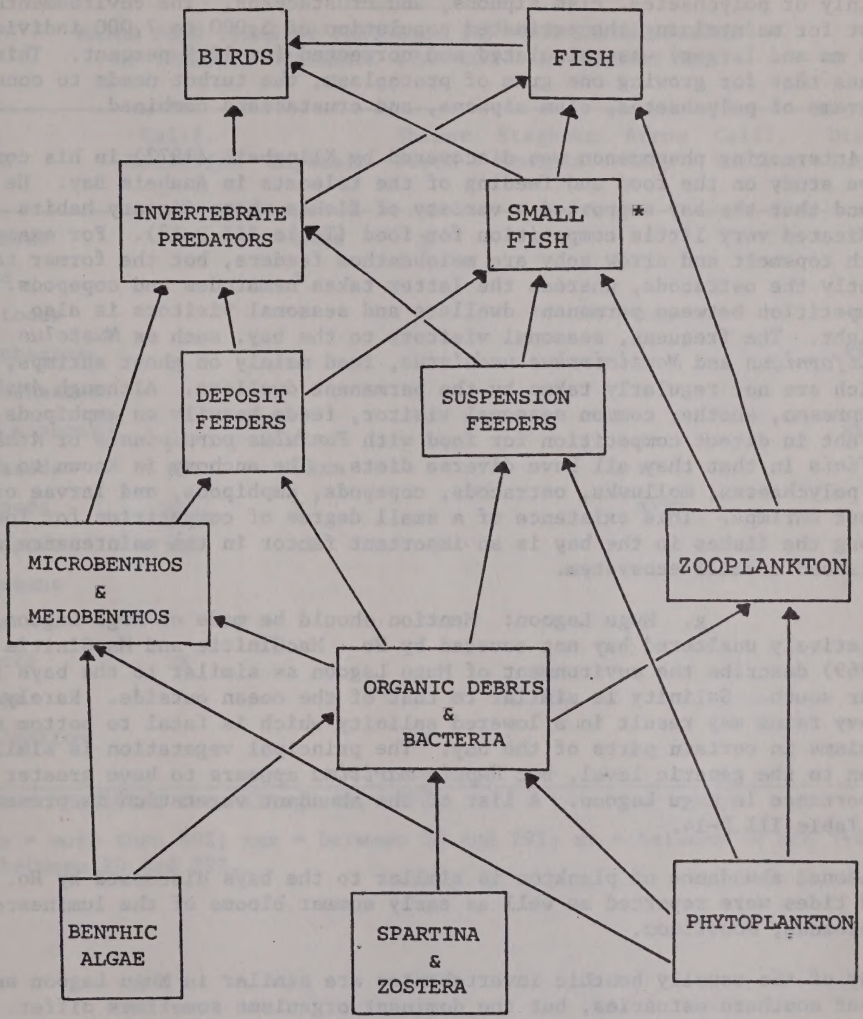
pelecypods, polychaetes, and crustaceans) in each square meter of mud bottom (Russell-Hunter, 1970). Maintenance of such a large production of benthos in the shallow areas of the sea is made possible through the abundance of food and nutrient in the areas.

Perhaps of major importance is the fact that the very productive shallow areas commonly have abundant particulate organic detritus and other forms of organic matter, clay-rich mud, bacteria, and detritus and suspension feeders, all within the photic zone. Basic nutrients released by bacterial decomposition are immediately available for fixation by the phytoplankton, algae, and other plants in the same area (Warme, 1971). There is no time lag as in deeper water, where nutrients released on the bottom must be brought into the photic zone by upwelling, overturn, or diffusion before fixing by photosynthesis. In the shallow coastal areas and embayments, the cycle is accelerated, and abundant food for the benthos results.

In areas shallower than 100 m (109 yards) zooplankton graze on only about 10 percent of the available phytoplankton (Williams, Murdock and Thomas, 1968). For instance, in an estuary where the estimated gross phytoplankton production ranges from 270 to 295 grams C/m^2/year (carbon/square meter) the estimated consumption of the primary production by the zooplankton herbivores is only about 30 grams C/m^2/year (Qasim, 1970). If it is assumed that most of the organic material produced in an ecosystem is likely to be consumed by the animal communities, then this large surplus of primary production must have been consumed by the benthic suspension and detritus feeders. Thus, benthic herbivores rather than zooplankton represent the critical herbivore link in the shallow-water food web (Figure III.D-14).

In the marsh area, the primary production is even higher. The estimated *Spartina* production in the salt marsh of Georgia is about 897 grams C/m^2/year (Teal, 1962), and in the area with *Zostera*, it is estimated up to 1,500 grams C/m^2/year in various parts of the United States (Mann, 1973). Odum and de la Cruz (1967) have shown that the buildup of microbial population on detritus, consisting of dead fragments of leaves and stems of *Spartina*, results in an increase in protein content from 6 to 25 percent of dry weight in detritus. Zobell and Felthm (1942) have also shown the importance of bacteria as food for animals dwelling in mud. Based on the counts of bacteria in cores 90 cm (35 inches) long taken from sediments in Mission Bay, they showed that there would be 1.1 gram dry weight of bacteria per cubic foot of sediment. Therefore, in a coastal embayment that is fringed with marshes and/or covered with eelgrass, the total productivity would be much higher than those without.

The rich benthic invertebrate fauna in the shallow areas in turn serve as food for the demersal fishes and shorebirds (Figure III.D-14). In his quantitative study on the diamond turbot of Anaheim Bay, Lane (1975) estimated that an average fish consumes about 3.34 grams/day of food consisting



* including anchovy, killifish, topsmelt, goby, etc.

Figure III.D-14. Generalized food web in the coastal embayments of Southern California (from various sources).

mainly of polychaetes, clam siphons, and crustaceans. The environmental cost for maintaining the estimated population of 5,000 to 7,000 individuals (50 mm and larger) was calculated and corrected for 12.9 percent. This means that for growing one gram of protoplasm, the turbot needs to consume 8 grams of polychaetes, clam siphons, and crustaceans combined.

An interesting phenomenon was discovered by Klingbeil (1972) in his comparative study on the food and feeding of the teleosts in Anaheim Bay. He found that the bay supported a variety of fishes whose dietary habits indicated very little competition for food (Table III.D-13). For example, both topsmelt and arrow goby are meiobenthos feeders, but the former takes mostly the ostracods, whereas the latter takes nematodes and copepods. Competition between permanent dwellers and seasonal visitors is also slight. The frequent, seasonal visitors to the bay, such as *Mustelus californicus* and *Menticirrhus undulatus*, feed mainly on ghost shrimps, which are not regularly taken by the permanent dwellers. Although *Anchoa compressa*, another common seasonal visitor, feeds heavily on amphipods, it is not in direct competition for food with *Fundulus parvipinnis* or *Atherinops affinis* in that they all have diverse diets. The anchovy is known to feed on polychaetes, mollusks, ostracods, copepods, amphipods, and larvae of ghost shrimps. This existence of a small degree of competition for food among the fishes in the bay is an important factor in the maintenance of a balanced coastal ecosystem.

g. Mugu Lagoon: Mention should be made of Mugu Lagoon, a relatively unaltered bay not covered by Ho. MacGinitie and MacGinitie (1969) describe the environment of Mugu Lagoon as similar to the bays farther south. Salinity is similar to that of the ocean outside. Rarely, heavy rains may result in a lowered salinity which is fatal to bottom organisms in certain parts of the bay. The principal vegetation is similar down to the generic level, but *Ruppia maritima* appears to have greater importance in Mugu Lagoon. A list of the abundant vegetation is presented in Table III.D-14.

Seasonal abundance of plankton is similar to the bays discussed by Ho. Red tides were reported as well as early summer blooms of the luminescent protozoan, *Noctiluca*.

Many of the usually benthic invertebrates are similar in Mugu Lagoon and other southern estuaries, but the dominant organisms sometimes differ. This is particularly true with the polychaete worms. Certain members of the Mugu Lagoon biota undoubtedly reflect a more northern component.

Table III.D-13

MAJOR FOOD ITEMS BY FREQUENCY (%)[a] FOR SEVEN SPECIES OF TELEOSTS OCCURRING YEAR-ROUND IN ANAHEIM BAY

FOOD ITEMS	Calif. Killifish	Topsmelt	Shiner Perch	Staghorn Sculpin	Arrow Goby	Calif. Halibut	Diamond Turbot
Detritus		xxxx	x				
Algae		x					
Nematodes					xxx		
Polychaetes							xxxx
Oligochaetes					x		
Clam siphons							xxx
Ostracods	xx	xxxx			x		
Copepods	xx	x			xxxx		
Amphipods	xx	xx					
Cumaceans							x
Crabs				x			
Insects	xx						
Gobies						xx	
Zooplankton			xx				

Source: Modified from Klingbeil, 1972.

[a]xxxx = more than 80%; xxx = between 60 and 79%; xx = between 40 and 59%; x = between 20 and 39%.

Table III.D-14

MAJOR ATTACHED PLANTS IN MUGU LAGOON

DIVISION - GENUS SPECIES
Thallophytes[a] (algae)
Enteromorpha intestinalis
Enteromorpha sp.
Rhisoclonium sp.
Ulva sp.
Spermatophytes[a] (flowering plants)
Water Plants
Ruppia maritima
Zostera marina
Marsh Plants[a]
Lower Marsh
Frankeria sp.
Limonium sp.
Salicornia biglowi
Salincornia pacifica
Spartina sp.
Triglochin sp.
Upper Marsh
Atriplex spp.
Botis sp.
Distichlis sp. (2 species)
Salicornia rubra or *S. depressa* (or both)

Source: MacGinitie and MacGinitie, 1969.

[a]The identification of the marsh plants was furnished by John E. Warme. Dr. Warme has since published the following paper: Graded bedding in the recent sediments of Mugu Lagoon, California. Journ. Sedimentary Petrology, Vol. 37, Eo. 2, pp. 540-547, Figs. 1-4, June, 1967.

Summary. There are 19 major coastal embayments in Southern California. Only three of them have remained relatively unaltered, Anaheim Bay, Upper Newport Bay, and Tijuana Estuary. Since very little biological survey of the marshes and bays has been done, a checklisted information of the flora and fauna of the area cannot be prepared.

The biota of Anaheim Bay are comparatively better known and probably represent a possible flora and fauna of the Southern California coastal embayments before alteration. Several species of fish utilize the bay for spawning and nursery grounds, and a great many species of birds use it as nesting, feeding, and shelter area.

Polychaeta is the single most studied group of organisms because certain species of them can be used as indicators of the bottom condition for monitoring pollution. A new form of extremely rare Crustacea was recovered from Anaheim Bay. It belongs to Cephalocarida, which comprise the most primitive living Crustacea of the world.

The existing condition of biological knowledge underscores the difficulty in understanding the ecosystem of the coastal embayments and their relationship with the total coastal ecology, since a biological inventory is lacking and only a few species are known to a level of quantitative characterization, e.g., biomass, density per unit area, environmental cost, and other factors.

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